PEARL

The Journal of HEREDITY

A SEX-REVERSING PALM

(SEE PAGE 485)

Giant Salivary Chromosomes Give New Clues to Gene

Five Generations of Toothlessness *Linked Genes in the Rabbit*

Inherited Udder Defects in Cattle and Swine

The Peopling of America *Index to Volume 25*

VOLUME 25 DECEMBER, 1934 NUMBER 12

The American Genetic Association

An incorporated organization devoted to promoting a knowledge of the laws of heredity and their application to the improvement of plants, animals, and human racial stocks

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COMING

Breeding Sweet Potatoes

In the temperate zone the sweet potato rarely flowers, but under subtropical conditions of temperature and length of day it is possible to obtain seed and breed new varieties. From the Sukhum Experiment Station in the Caucasus two new species crosses are also announced.

Growth Influence of the Thymus Gland

An influence that is exerted, not on the individual treated, but in the *next generation*, has great theoretical interest to geneticists, and no little practical importance in demonstrating that this heretofore mysteriously "useless" gland has a profound influence on growth rates.

Selective Fertilization

Preference in selection of mates is generally observed among animals and from the time of Darwin such sexual selection is conceded to have important, though undetermined, evolutionary implications. Do gametes also have a certain "freedom of choice" and what part does this play in evolution?

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"PORTRAIT" OF A SALIVARY GLAND CHROMOSOME

Frontispiece

Ever since the gene hypothesis was generally accepted, geneticists and cytologists have dreamed of the day when it would be possible to see the actual genes, instead of having to be satisfied with studying their "shadows," which were "reflected" in the morphological development of generations of organisms. Giant salivary gland chromosomes of the fruit fly (*Drosophila melanogaster*), whose study is the subject of the accompanying article, are proving to be a new genetic tool of the utmost importance. The chromosome illustrated here is the right arm of the third chromosome—the light and dark bands and areas represent a definite pattern, which can be identified in any third chromosome, this pattern having an astonishing uniformity, somewhat as the pattern of a spectrum is characteristic of a given kind of light. Just what these bands are, and just where the actual genes are located is still not determined, but some of them have been "bracketed" in very small regions—close to, if not actually on, some of the dark bands (see Figure 4).

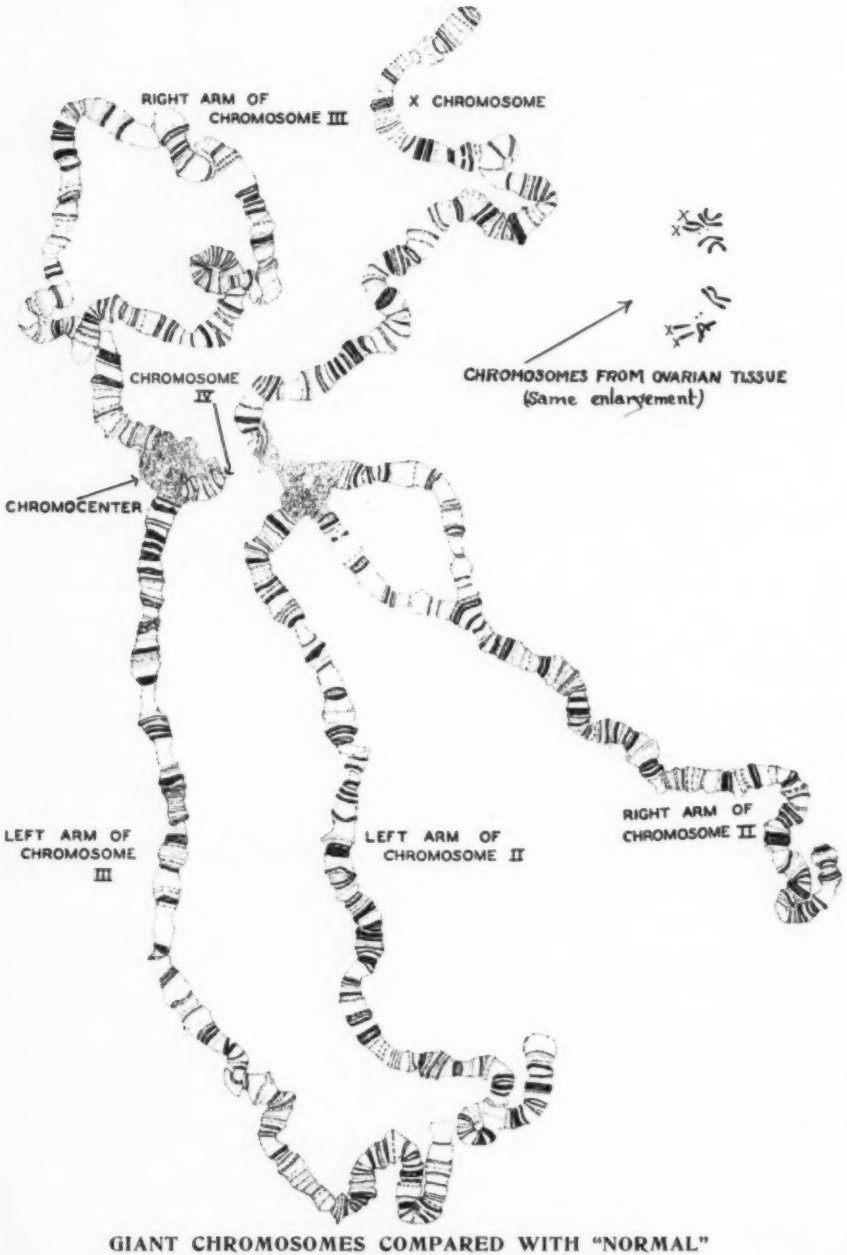
SALIVARY CHROMOSOMES AND THE ATTACK ON THE GENE

THEOPHILUS S. PAINTER
University of Texas

EVER since the formulation of the chromosome theory of heredity cytologists and geneticists alike have dreamed of the day when some one would find somewhere an organism in which the chromosomes were so large that it would be possible to see qualitative differences along their lengths corresponding to the different genes which we know must reside there. With the methods and material in common use up to two years ago, the realization of this dream seemed very remote. With the best of optical equipment, very refined techniques and detailed studies by the most competent observers over the world, little was to be seen at the time of nuclear division except deeply staining rods, *v*'s or *j*'s; if earlier prophase stages were examined, knotted strands or threads. Patient work had revealed in both of these stages abundant evidence for the individuality of the chromosomes, but for any single element the landmarks were few and really of little practical value. My own work on chromosome rearrangements and the plotting of chromosome maps of *D. melanogaster,* as well as the splendid work and maps of Dobzhansky, had convinced me that if any real progress was to be made in this field we would have to use new material and possibly devise new methods from those which had heretofore been in common use. Where was this new material to be sought?

All cytologists have known for a long time that in the salivary glands and other tissues of the larvae of Diptera in general there occurs what has been called a "permanent spireme." In the nuclei of such tissues structures called chromosomes are very large and show very conspicuous bands or disks of deeply staining material alternating with clearer areas. (In the following paper I shall call these structures bands without prejudice as to their real nature). No one knew, however, whether these banded elements corresponded to the elements seen in the metaphase plate or were nuclear differentiations related, in some way, to the functional activity of the cells. In looking for new material for a study of chromosomes it was quite natural that I began by investigating the possibilities of the large structures found in the salivary gland of *D. melanogaster.*

Work was begun in the early fall of 1932. The first problem was to develop a technique for separating the elongated threads intertwined within the nuclear wall, so that they could be studied. This did not prove a very difficult task, indeed, we are frequently able to separate a whole element from the nucleus. (See especially Figure 1 and the photomicrograph of the right arm of the third chromosome). The chromosome consists of an elongated more or less cylindrical rod made up of lightly staining material, while running apparently across each may be seen a great variety of "bands," some broad and deeply staining, others narrow or made up of a series of dots. A study was begun at once to determine if the patterns of bands and lines, which are so conspicuous, were constant morphological characteristics of a given element. It turned out that the landmarks are constant to a most extraordinary degree so that we were able to recognize the same element in the nuclei of different individuals and ultimately to follow any characteristic bit of a chromosome as it is shifted here and there to other chro-



GIANT CHROMOSOMES COMPARED WITH "NORMAL"

Figure 1

The main figure is a camera lucida drawing of the elements found in a salivary gland nucleus of a female larva, showing the chromosomes just as they lay on the slide. The chromocenter material, to which all elements or arms are apparently anchored, is composed of inert chromatin. All homologous elements or parts have undergone somatic synapsis except

(Continued on next page)

mosomes through the agency of irradiation.

After the individual chromosomes had been studied until each element could be recognized, we were confronted by an enigma. The fruit fly has eight chromosomes consisting of four pairs of like elements. In salivary gland nuclei there are six chromosomes which are all attached to a common substrate. These six elements are individually quite distinct, five being very long and one quite short (see Figure 1). The short element, we guessed, represented the dot-like fourth chromosome of metaphase plates, but why was it single? After all, did these nuclear structures really represent the chromosomes as we know them at metaphase?

Obviously the next step was to study some chromosome rearrangement which would allow us to identify an individual element. The one selected is known as the "forked-Bar" break, discovered several years ago by my colleague, Mr. Wilson Stone. My own earlier cytological study of this break[7] had shown that the metaphase *X* chromosome was broken into two approximately equal parts. Female larvae homozygous for the aberration were examined and in the salivary glands one of the six elements was broken and thus we could identify the broken element as representing the *X* chromosome. But there were two puzzling features in this case; first, there was only one *X* element in the cell and, second, the break was not in the middle of the *X* but well towards one end. The final elucidation of this case led to two separate discoveries, both essential for an understanding of the condition existing within the salivary gland. One is the occurrence of somatic synapsis and the other is a realization that, in salivary glands, it is the relatively active genetic part of the chromosome which shows the banded form.

The discovery of somatic synapsis was forced on me by the following considerations. The larva studied was a female and hence must carry two sex or *X* chromosomes. Therefore the element identified as the *X* must be bivalent in nature. It had been observed when studying small salivary nuclei, at the beginning of this work, that often an element showed, as I then thought, the prophase split. It was now clear that what had been seen was a step in a fusion process. Just why the forked-Bar break came so near to one end in the salivary gland did not become clear until later.

Once the *X*'s and, by inference, the fourth chromosomes were known, by means of chromosomal aberrations, involving the other elements, the remaining chromosomes were identified. It is to be noted that in the salivary gland the two arms of the second and third chromosomes, respectively, appear as separate elements.

With these four discoveries before us (i. e., constant and distinctive patterns, somatic synapsis, the behavior of active and inactive regions and the separation of the arms of the large autosomes) it was clear that we had within our grasp the material of which every one had been dreaming. We found ourselves out of the woods and upon a plainly marked highway with by-paths stretching in every direction. It was clear that the highway led to the lair of the gene.

Legend to Figure 7 (continued)

the right arm of the second chromosome near the point where this is attached to the chromocenter. By checking one can see that the patterns of the unsynapsed parts are similar. The synapsed fourth chromosomes are somewhat bent and more or less covered by chromocenter material.

In order that the reader may compare the salivary gland chromosomes with the chromosomes of *D. melanogaster* that have been studied heretofore, in the upper right hand corner of this plate are two camera lucida drawings of these chromosomes as they appear in the ovary. When we take into consideration the inert chromatin, the salivary gland elements are over 100 times as large as the oogonial elements. Actual measurements give a ratio of 1:110

Upon consultation with my colleagues, it was decided to withhold publication until we had at least looked at the house in which the gene lives, and explored some of the by-paths. We all well knew that at the first hint of these discoveries Drosophila workers over the world would rush into this field and exploit it, and we desired that the credit for both the discovery and the orderly presentation of the main facts should come to the University of Texas. My colleagues, Dr. J. T. Patterson, Mr. Wilson Stone, and Dr. Patterson's technical assistants Miss Bedichek and Miss Suche, isolated and genetically analyzed hundreds of translocations which were placed in my hands so that really worthwhile cytological maps of Drosophila chromosomes could be presented. I wish to stress that, aside from the initial discovery, what has been accomplished here is largely the result of scientific cooperative effort in its very best sense. To my colleagues named I hereby express my obligations.

To date five papers or reports have been published by the writer and one by a student working under him. I have three articles now in press. At the invitation of the Editor of the JOURNAL OF HEREDITY it is proposed to give a summary of what has been accomplished here at the University of Texas, up to the date of this paper. If the information given is not covered by my published works I shall indicate it as in press or unpublished data.

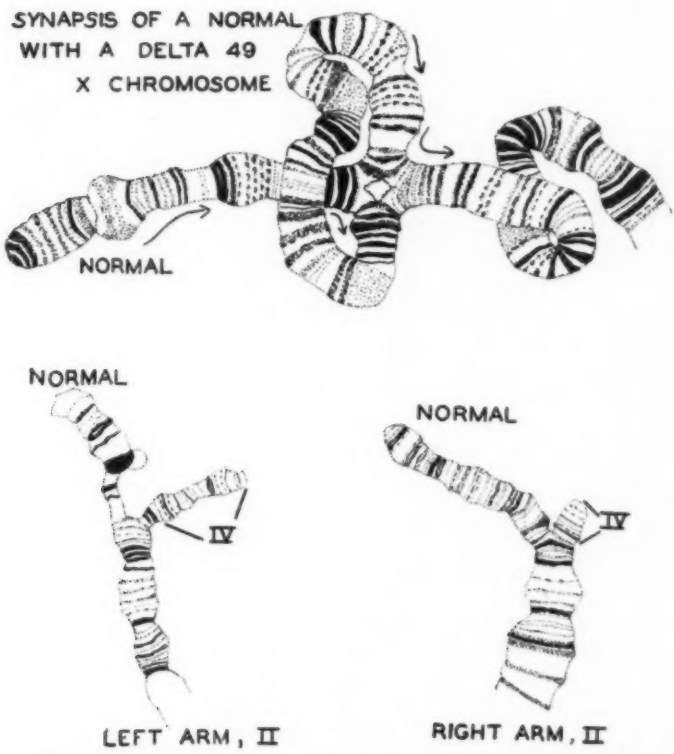
How the Position of a Gene Is Located

The first step in the location of genes and the plotting of cytological maps is an accurate knowledge of the morphological characteristics of each chromosome or arm. This is gained by a careful study of normal chromosomes. In many regions of the chromosomes the patterns are extremely complex and often the lines are extremely fine. This being the case, the reader must realize that the figures I have given of the various elements may contain minor errors. In some cases extremely fine details have been omitted. We are dealing with labile material, and while as a whole the patterns are very constant and definite, different degrees of staining and doubtless different preservations and stains may somewhat alter the image. Certain regions of certain definite chromosomes seem somewhat variable. In my several papers I have called attention to these cases.

Once the normal morphology is known, the fact that homologous chromosomes or parts undergo an intimate union, during which they pair up line for line, band for band, is of the very greatest service in determining the position of gene loci. This process I have termed "somatic synapsis" and it must not be confused with the tendency of homologous chromosomes of all Diptera to lie together in metaphase plates, though in the end, both processes may be the expression of the same force. As a result of somatic synapsis two homologous chromosomes unite into one apparently single structure.

There are three general ways of determining the position of gene loci. Simple mutual translocations or inversions in which we know genetically between what genes the break or breaks have occurred; short deletions where we know what genes are missing; and a study of a series of breaks all falling between the same two gene loci. These will be taken up in turn.

When we study a larva heterozygous for a normal, and a broken chromosome, we find that, beginning usually at the spindle fiber ends, the normal and aberrant elements synapse line for line, band for band, up to or nearly to the point where the latter is broken, where the aberrant element (if we are dealing with a mutual) diverges. By comparing the adjacent patterns of the two elements it is easy to determine where the break has occurred. Knowing which two genes are separated by the break, we can



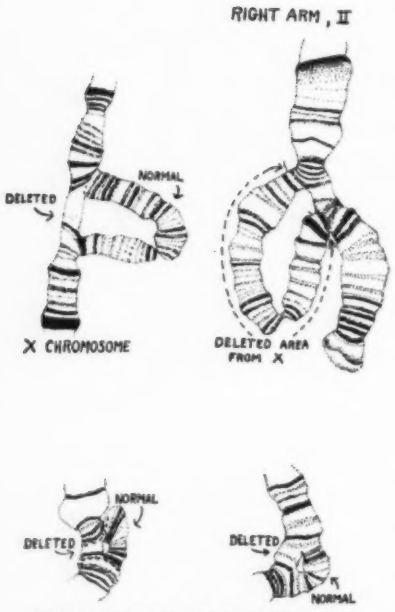
SYNAPSIS OF NORMAL AND INVERTED CHROMOSOMES

Figure 2

The upper figure is a camera lucida drawing, taken from a female larva, which was heterozygous for a normal and a "delta 49" *X* chromosome. Synapsis has been complete except at the points where the delta 49 *X* is inverted. The extreme right hand ends of the paired *X*'s are not shown.

The two lower figures are camera lucida drawings to illustrate the way the point of breakage of a chromosome is determined. In each example, the normal element lies on the left and the aberrant one to the right. The aberrant element synapses with the normal right up to the point of breakage. These two cases involve a mutual exchange with a fourth chromosome. The latter is indicated in the drawings.

place these to either side of the point of breakage. Figure 2 illustrates cases of this sort, in addition a figure of an inversion (delta 49) in the *X* chromosome is shown. This method is relatively crude; nevertheless, by using it I was able to circumscribe a number of genes along the *X* chromosomes within the confines of an area covered by two or three bands. It was realized very early that short deletions would be more serviceable for the exact location of genes, and fifteen months ago, Mr. Mackensen, working under my direction, began a study of short deletions. The method was clearly indicated in my abstract given to the American Society of Zoologists and appeared early in December, 1933. At the meetings of the Genetics Society of America, 1933, Mr. Mackensen gave in his abstract both the method and his results up to that time.



SYNAPSIS OF DELETED AND NORMAL CHROMOSOMES

Figure 3

These are camera lucida drawings showing the appearance of deleted and normal *X* chromosomes after they have undergone somatic synapsis. The upper left hand figure shows the normal and deleted *X*, while the figure to the right shows the deleted area inserted into the right arm of the second chromosome.

The lower figure shows short sections of normal and deleted *X*'s after somatic synapsis.

When a normal and a deleted chromosome synapse they usually pair throughout their lengths except in the region of the deletion, where the normal element usually buckles. Figure 3 illustrates cases of this type, drawn by Mr. Mackensen and used by me with his consent. It is very fortunate that as a result of irradiation, as my colleague Dr. Patterson has shown,[6] short deletions are extremely common; knowing then what genes are missing and what bands are lacking we can say that the missing genes lie somewhere in the deleted area. We had in our stocks a number of deletions isolated by Dr. Patterson. These were given to Mr. Mackensen for study and since then Mr. Mackensen has isolated many cases of his own.

The third method is to study a number of breaks which have occurred between genetically adjacent gene loci. It has been pointed out elsewhere by my colleagues[17] and in my study of the third chromosome (in press) that translocations between the fourth chromosome and the large autosomes are often bunched within narrow limits both morphological and genetic. Mr. Mackensen has isolated two deletions which removed the locus of vermilion, these overlapped a little so that Mackensen could restrict the locus of vermilion to the left part of a broad compound band. (See Figure 4, *X* chromosome). Mr. Mackensen's study is now in press.

By the simple methods outlined, cytological maps of all the chromosomes of *D. melanogaster* have been produced, and in Figure 4 the maps, as they stand at the moment of writing, are reproduced. Especial attention is called to the map of the *X* chromosome. Above this figure lines show breaks which have allowed me to restrict the positions of loci. Below the figure I have indicated further localization of specific genes by Mr. Mackensen. Full credit is due Mr. Mackensen for this work, which is now in press. It will be seen that there are large uncharted areas along all of the maps of the autosomes, but this laboratory proposes to concentrate its efforts for the next year or two in filling in the gaps. Other investigators will, it is hoped, pursue the same line of work so that ultimately we shall know the locus of every known gene.

Where Are the Genes?

The methods have been described by which it has been possible to restrict the morphological position of gene loci to the area covered by one or even a part of one of the deeply staining bands on the *X* chromosome. Where then are

the genes? Are they represented by the deeply staining material or by some other part of that region of the chromosome? To answer these questions we are led to a consideration of one of the oldest problems in cytology, namely, the ultimate structure of these cross bands and of the chromosomes. At this point I wish to state that while I have used the term "band" in all of my papers, I was very careful to state in my article in *Science*[6] that these cross striations "appear to run around an achromatic matrix." As to the ultimate nature of these "bands," I have not been, nor am I now, willing to commit myself finally.

Earlier Work

So far in this account little mention has been made of the work of other investigators because we have been utilizing and interpreting morphological structures in terms of modern genetics. The application is new, but much of the morphological background has been known for a long time. Several investigators have examined the chromosomes of *D. melanogaster*. In this JOURNAL, Kostoff published a photograph of these discoidal chromosomes in 1930, and in 1931 Kaufmann described these elements. Both of these studies were mainly morphological and did little more than show that in *D. melanogaster* the conditions were much the same as had been described for other dipteran chromosomes.

As I was in the midst of my first year's work, an article appeared by Heitz and Baur[2] dealing with the salivary chromosomes of *Bibio hortulanus*. There are 10 chromosomes in this fly but in the salivary glands there are only five. Each of these five is made up of two elements which, as the figures show, are twisted together. At times the union appears more intimate. Heitz and Baur did not regard this union as of any particular importance, apparently. However, they did make it clear that partner strands were morphologically alike in the arrangement of the bands, and they state that each of the five groups of chromosomes can be recognized from cell to cell on the basis of length, association with a plasmosome, the shape of the ends and the pattern of the bands. No genetic application of these facts was made by them.

Again in a paper[3] which appeared later in 1933 Heitz figured parts of the chromosomes as they appear in the salivary gland of *D. melanogaster*, but this work need not concern us here.

Balbiani in 1881 was the first to describe the banded chromosomes in the salivary gland nuclei of the larvae of the Chironomus fly. Within these nuclei he found a long thick thread which showed throughout its length cross striations or bands. Balbiani interpreted these cross striations as disks of deeply staining material and he conceived of the chromosomes as being made up of disks of chromatin and what he called a "zwischensubstanz" or in modern terms, matrix or plastin.

At approximately the same period Leydig (1883) also worked on larvae of Chironomus; he saw the cross striations on the chromosomes, but he interpreted their structure and that of the chromosomes in quite a different way. According to Leydig "the cross striations are restricted to the periphery of the thread cylinder without cutting through it or having connections through it." (The writer's translation of a passage cited by Alverdes[1] p. 173). He describes the cross striations as showing shallow indentations "put together out of small sticks comparable to the elements of muscle disk." "The finer dividing lines of the dark striations formed by the little sticks are stretched out through the light between zone (zwischenzone) so that we get the impression of faint longitudinal lines being present." (The writer's translation of passage cited by Alverdes[1]).

In 1884 Carnoy described the presence of cross striations in a number of Arthropods. He conceived of the chromosome as being made up of a hollow

cylinder of plastin on the inner wall of which the chromatin was deposited. When the chromatin is localized in definite areas, the cross striation effect is produced. Carnoy saw the chromatin of the dark areas divided into short segments and granules. In some forms Carnoy found that the chromatin lying on the inner wall was arranged in a corkscrew fashion, so that a spiral thread of chromatin ran from one end of the cylinder to the other.

In 1884 Korschelt published upon the structure of the chromosomes in Chironomus larvae and he visualized the condition observed in this way: The chromosome is not made up of alternate layers of material but the cross striations are due to an optical effect. There are ridges and valleys running across the chromosome and with transmitted light these give the impression of light and dark bands.

After this early period, comparatively little was added to our knowledge of the banded chromosomes until 1910 when van Herwerden took up Chironomus again. She thought the cross striations were due to the presence of a spiral band or rod of chromatin running around an inner axis.

Shortly after this Erhard (1911) studying the same type of material concluded that the chromosome was made up of alternate disks of light and deeply staining material.

The next study which requires our attention is that of Alverdes[1] in 1912. (References to work cited above are given by Alverdes). As we have seen there were two general explanations for the crossbands on Chironomus chromosomes, one was that they were due to disks or rings of chromatin separated by relatively clear material, and the other was that there was a spirally wound chromatic thread running in some way from one end of the chromosome to the other, and that the banded form was the result of viewing the imperfectly preserved spiral from the side. Alverdes proposed to settle this controversy by studying the way in which the crossbanded chromosomes arose in the ontogeny of the individual. He found in the earliest stages of the salivary gland that the chromosomes showed the usual chromomeric structure, that is, were made up of little knots of chromatin lying along a thin thread. As the nucleus enlarged, the achromatic matrix increased in thickness and adjacent chromomeres sent out processes and ultimately fused so that in the end a typical spiral chromonema thread was produced. Subsequently, these chromomeres, or at least parts of the chromatic spiral, separated forming heavy disks which by subdivision later formed narrower disks which frequently appeared as a series of more or less connected dots running around the chromosome. The numerous detailed drawings which Alverdes gives of this period show a large number of lines or striae running through the clearer areas between the more darkly staining landmarks. Thus it will be seen that Alverdes would explain the various interpretations given for the structure of Chironomus chromosomes as being due largely to the age of the larvae studied.

Kaufmann[4] has discussed the probable relation between the discoidal bands on the salivary chromosomes of *D. melanogaster* and the chromonema theory of chromosome structure and he concludes "that the appearance of the discoid or discontinuous structure is the expression of an inadequate technique, the spiral bands presenting a more accurate picture of the normal arrangement of the chromatic material." (p. 556).

The Structure of the Salivary Chromosomes

This was the status of the question of the nature of the cross-bands, principally in Chironomus, when I began work. The picture before me, in *D. melanogaster* was so like what the earlier workers had described that there was little doubt in my mind as to their ontogenetic and structural similarity. Although I have used the word "bands"

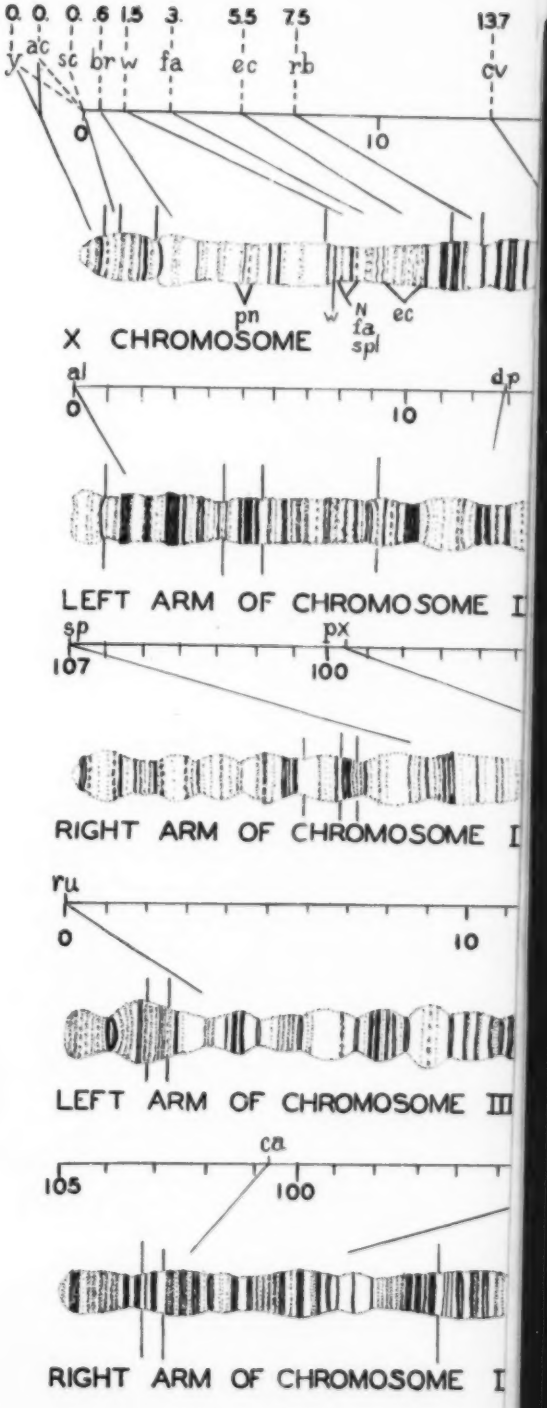
CYTO-GENETIC MAPS OF SALIVARY CHROMOSOMES

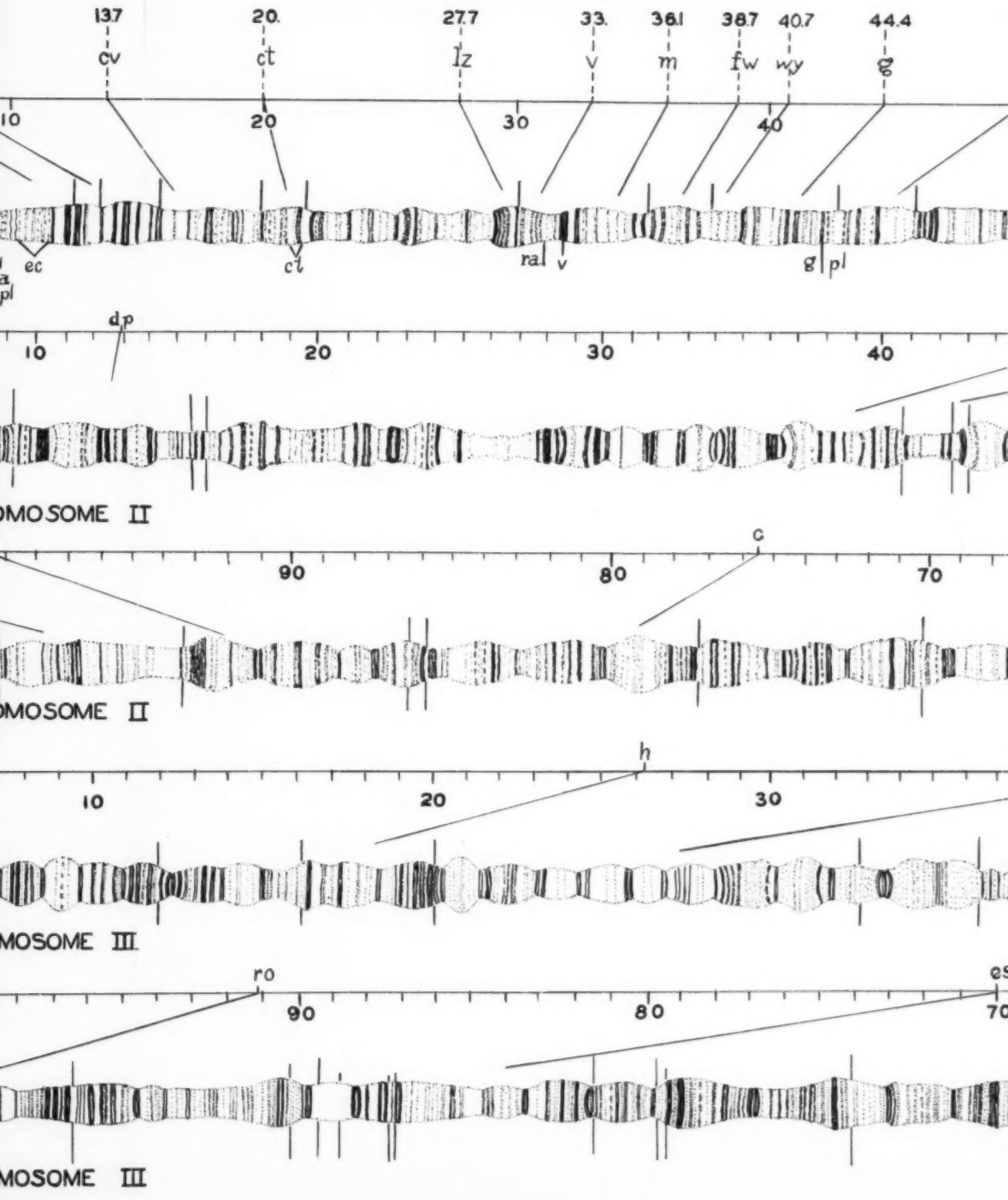
of *Drosophila melanogaster*

Figure 4

The figures on this plate show the typical morphology of the chromosomes and the position or morphological limits of all gene loci upon which we have data at the time this paper was sent to press. In my several papers I have indicated how these figures are made up, the effect of different degrees of staining or different stains on the image observed, certain regions which appear to vary between two patterns, and other factors to be considered. All of these chromosome charts err probably in that undue prominence is given to minor details, an error scarcely to be avoided in pen and ink sketches. In some cases fine details have been omitted, either because they have not been completely worked out or because they are so faint in ordinary preparations. Nearly all lines and bands are double or more complex in nature. Few bands are really continuous, but in lightly stained preparations are broken up into smaller units. One can usually count from five to seven units across the surface of the chromosome. The scales above the chromosomes represent the crossover maps. The symbols are those of genes whose position or whose morphological limits are indicated by breaks or deletions. The lines next the chromosomes show the approximate position of the breaks. Lines from the crossover maps to the elements or arms indicate on which side of the break the gene locus must lie.

The *X* chromosome has been most thoroughly studied. The two arms of the second chromosome are orientated so that the spindle fiber ends of both lie to the right. It will be noted that in both arms the chromosome extends some distance beyond the last known gene marker. For example, in the right arm of the second, the gene speck which lies farthest to the right on this arm of all known genes, is still far removed from the end of the arm, morphologically. If the bands represent gene-bearing areas directly or indirectly, there must be many unknown genes in this third chromosome. These drawings are copied and modified from charts which have either been published or are in press.

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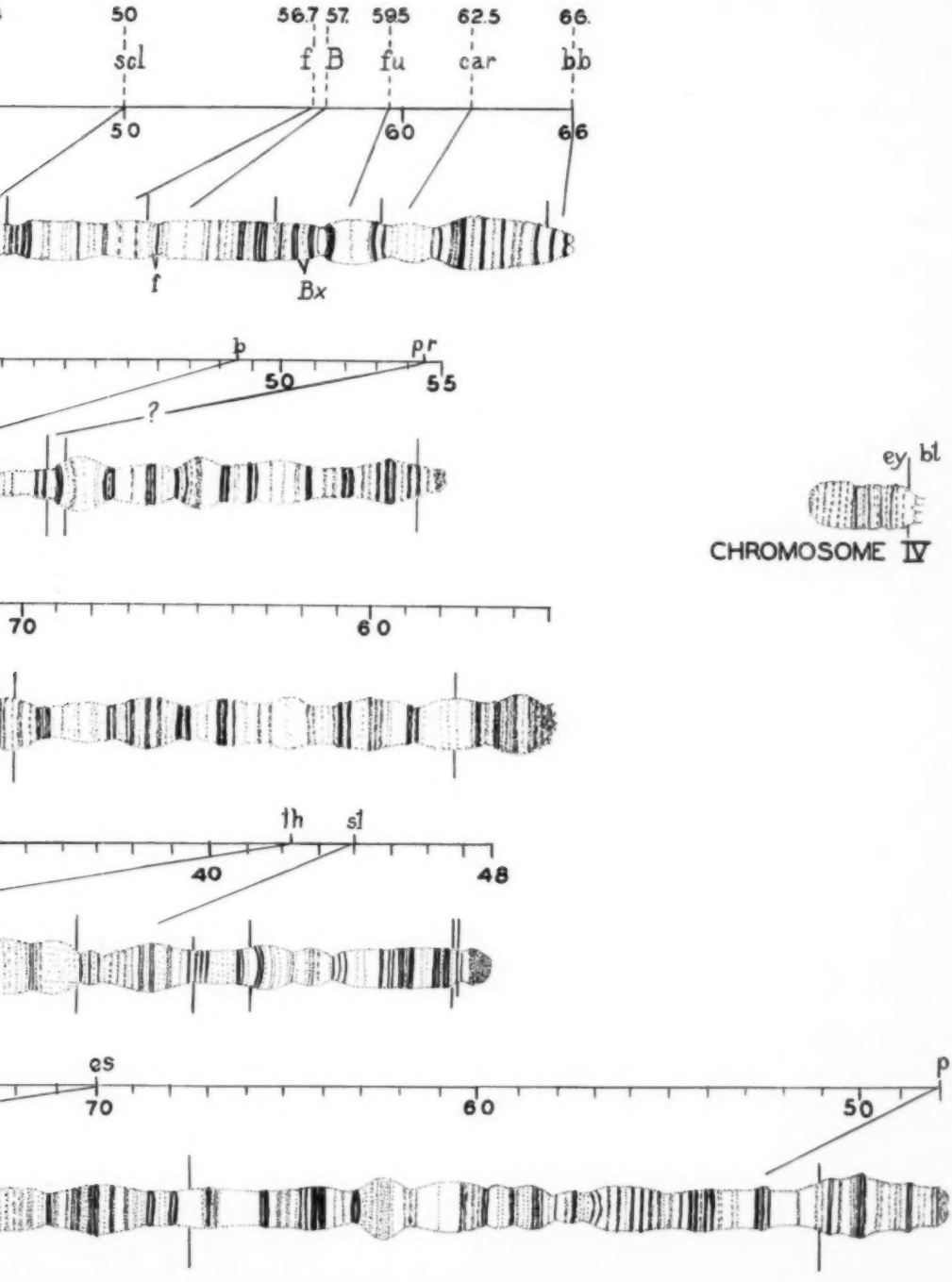
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to describe the deeply staining landmarks, the most superficial examination of a lightly stained chromosome shows the bands to be made up of smaller parts. Any of my drawings, except the schematic ones, will show much evidence of this. Even the heaviest bands have crenelated edges just as Leydig described, and the lighter ones appear to be made up of from five to seven smaller areas running dash-like across the uppermost surface of the chromosome, making a total of more than double these numbers. This appearance is best seen on the fourth chromosome. In my paper which appeared in May, 1934, I called attention to the latter fact, and stated that in a later article I would take up the question of the nature of the chromosome, in detail.

As a result of my observations on somatic synapsis I knew that the apparent single chromosomes were composite in nature and represented the union of at least four similar strands very closely apposed to each other. (The two homologues which unite in somatic synapsis often show in turn prophase splits). It therefore seemed to me that little more was to be gained by a direct study of these cross structures in old larvae. Who can say whether we are dealing with disks or with rings, because four closely apposed rings viewed from the side would look like disks running through the composite chromosome. The safer avenue of approach appeared to be the ontogenetic. When we know how the constituent parts of the simple unsplit and unsynapsed elements arise, then we can more certainly interpret what we see in the cross bands of old larvae. This is what I had in mind when I wrote[12] in the summer of 1933: "Foremost stand questions about the intimate structures of chromosomes, whether the chromatic bands lie on or within the matrix? What part carries the genes? What is the relation between the genes and the chromatic substance? and a host of similar questions. From the first, such questions have dominated our interest in these studies; but as tempting as it may be to speculate upon them, at present it seems unprofitable to consider these points until we know more about the genesis and ontogenetic history of these peculiar chromosomes."

In the fall of 1933 I set one of our graduate students, Mr. Sigmund Hayes, to work on the early history of these peculiar chromosomes. Our preliminary study was brought to a close this past summer. As far as we have been able to determine, we do not have in *D. melanogaster* the series of complicated changes in the chromosomes described by Alverdes for Chironomus. The earliest stages show small chromomeres lying along a relatively achromatic thread. As the nuclei increase in diameter, the threads hypertrophy and we can see more and more details. Whether these details become visible just because of their size, or whether the chromomeric thread is undergoing changes is not known. I rather expected to find that the chromomeres of the earlier stage would prove to be "compound chromomeres," in the sense that Belling used this term, and that these would spread out, in some way, along the matrix giving the final pattern, and that what Alverdes had seen were steps in this process. A great deal needs to be done and the nature of the problem requires the best optics and a very intensive study of minute details.

Mention has been made in the popular press recently of the work of Dr. Calvin B. Bridges in this field based on a lecture given at Woods Hole, Mass. Since some of the short accounts are misleading, out of fairness to Dr. Bridges, and to myself the following statement is made with the knowledge of Dr. Bridges and based on a personal letter from him. Following my lead, Dr. Bridges took up a study of salivary chromosomes in December, 1933. He confirms my work on the constancy of

pattern down to the finest detail and has directed his efforts among other things along three lines: (1) By studying chromosome aberrations, he has been able to localize three genes in the right arm of the second chromosome to an area covered by four bands. (2) He has made a detailed census of the lines on the *X* and fourth chromosomes. (3) From a detailed study of the cross bands he concludes that they are made up of unitary components apparently definite and usually sixteen in number. The dots and dashes visible as light lines are arranged longitudinally in spiral rows so that we have the effect of a twisted cable made up of 16 strands.

It would be out of place to discuss the work of Dr. Bridges in advance of his paper (in press in U. S. S. R. and a Carnegie report), which it is hoped will not be long delayed in publication.

As the final draft of this paper was being typed a short article by Koltzoff has come to hand (*Science*, Oct. 5, 1934), giving his views on the structure of the salivary chromosomes of *D. melanogaster*. Like Bridges, Koltzoff thinks that these chromosomes are made up of 16 strands running spirally the length of the chromosome. Without going into the question at this time, it may be remarked that the morphological observations on which both men, apparently, base their ideas of chromosome structure are much like those reported by Leydig somewhat more than half a century ago.

To return now to the question of where the genes are, let me emphasize that so far we have been able to show that they reside in that area of the chromosome covered by one or a part of one band. We have no definite proof that they are a part of any of the structures which have been seen in these bands: they might lie in the matrix. But since the bands are obviously particulate and show a complex structure, it seems more probable that the genes are to be sought here. But after all, as the Editor of *Science News Service* aptly expresses it: "Whether these tiny units are the genes themselves, or only the 'genophores' or gene bearers, is a matter of relative unimportance. The important thing is that they have been unveiled, so that the searching finger of science may probe a little further into the secrets of life." (Sept. 29, 1934, p. 196.)

By-Paths

We have stressed, in the foregoing pages, how the salivary chromosomes have allowed us to trace the genes to definite regions of the chromosomes, and this is, perhaps, from a theoretical point of view, the outstanding feature of the work to date. There are, however, a number of both related and unrelated problems which can be attacked by this new method. Some of these will be briefly discussed.

Because the new cytological maps are really pictures of the several chromosomes with labels showing the approximate or exact location of many genes they can be used very advantageously for the study of all types of chromosome rearrangements. These maps really take the guess-work out of a genetic study of chromosome aberrations and give us a very much more accurate picture of what has occurred than could be obtained by any but the most exhaustive breeding tests. This is true of simple mutual translocations and especially of complex rearrangements which are proving much more numerous than was first suspected. Once a translocation or deletion is isolated, a cytological examination of heterozygous larvae allows us to read right off just where the break is with reference to known gene loci, or what parts (and genes) have been deleted. Ordinarily, this can be done within an hour after the larvae is killed, often in much less time. The practical value of the new maps for this type of work can scarcely be overestimated.

Again, as a by-product of the X-ray work, is the realization that in many

cases the formation of new species is preceded by some type of chromosome rearrangement which sets up a physiological isolation within the parent species. By crossing *D. melanogaster* with *D. simulans*, for example, and examining the salivary chromosomes of the hybrid larvae, we can tell at once just what rearrangements have occurred. In this way, we are now preparing a full set of maps of *D. simulans* here at the University of Texas. The possibilities of this type of work seem unlimited. Perhaps equally valuable, from the evolutionary standpoint, is the fact that with the salivary chromosome method we can make a careful study of the effects of various aberrations on the individual, e. g., the duplication of short pieces.

Spacing of the Genes

Another field upon which this new method has thrown light is crossing over. Thanks to somatic synapsis we can actually see how the chromosomes and genes pair in diploid and triploid cells and we now enter an era of testing out some of the speculations with which this general field is overrun. One example will suffice to illustrate what can be done. Long ago, Dr. H. J. Muller called attention to the bunching of the genes along the chromosomes. In one case at least, this seems to have a simple explanation. In the *X* chromosome (see Fig. 4) from crossveinless on the right, the crossover map and the cytological map agree rather closely. But to the left of crossveinless the genes tend to be much farther apart physically than they are on the crossover map. The explanation would seem to be simple. As we approach the left hand (free) end of the *X* there is actually less crossing over per physical unit than in the middle (due possibly to the fact that the strands slip out to the end rather than break) and so the bunching of genes is not real but only the effect of reduced crossing over. The same method of approach has been used to explain other crossover phenomena in various papers now in press by my colleagues and by myself.

A study of the second and third chromosomes has led to the discovery that both of these elements carry relatively inert material in the region of the spindle fiber. We have been able to confirm and prove, by genetic and cytological methods, the brilliant work of Heitz in this field. A good deal of the material which we see in the metaphase chromosomes does not carry any known active genes. (For full discussion of this topic, see my study on the third chromosome, now in press.)

Finally, mention should be made of the work now in press (Painter and Stone) dealing with the fusion of the *X* and fourth chromosomes. It has been found that about half of the translocations between the *X* and fourth chromosomes are really fusions at or very close to the point of spindle fiber attachment. Similarly, many translocations between the second (or third) and fourth chromosomes are simple exchanges by which one whole arm is replaced by a fourth, and the displaced arm persists as an independent element. The theoretical aspects of these cases (see paper in press) have a broad bearing not only on the more general problem of chromosomes and speciation but on the nature of the mitotic spindle itself.

In this review it has been possible to touch only the high spots of what has been accomplished since this new lead was taken up and the salivary chromosomes made available for study. New vistas open before us on every hand. But after all is said and done we must realize that the utilization of these giant chromosomes for solving many vexing problems of cytology and genetics is comparable to the forging of a new tool and the important thing is to *use* this tool. Like the X-ray, it is a new method of attack and, while we can scarcely

hope that the results which may follow will have as profound an influence on biology as Dr. Muller's discovery, it is nevertheless clear that cytology, as a science, enters a new era in its development.

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✦

Discovery of "Position Effect" Through Use of Salivary Gland Material

Dr. H. J. Muller, who during the past two years has been a guest of the Soviet Government, reported on October 25 most interesting results with a combination of the X-ray technique and cytological observations of salivary gland material. In cooperation with Dr. A. A. Prokovyeva, Dr. Muller has studied intensively the region of the scute series of genes near the end of the X-chromosome (see Figure 4). The fact that the scute "gene" was in reality a closely grouped series of "step allelomorphs" was reported in the Journal in 1930.* By using induced breaks in the region of scute, Muller and Prokovyeva have been able to determine very exactly the *locus* of several of these scute elements. Such accurate mapping, combining the cytological approach and the genetic would be out of the question with any known material except salivary chromosomes.

One of the most interesting developments of this research is that Muller and Prokovyeva have detected a "position effect" depending on the relative location of the scute genes. Translocations of the scute genes from the normal position, so that they lie next to new gene-neighbors in the chromosome produce flies so different in appearance that they would be classed as mutations. This effect apparently operates through a very short distance on the chromosome but it appears to be proven that the effect is due to the propinquity of the genes, and not to other differences in the genic material. If it is found that this "position effect" is a principle of general application, it may prove of tremendous signifiance in giving us a clearer understanding of the gene and the way in which it operates to control the development of morphological characters.—R. C.

*Serebrovsky, A. S., and N. P. Dubinin, X-Ray Experiments with Drosophila, *Journal of Heredity*, 21: 259-265. 1930.

LINKAGE OF "WIDE-BAND" AND "AGOUTI" GENES

The Agouti Gene and a Modifier Shown to Be Situated on the Same Chromosome in the Domesticated Rabbit

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Brown University and The Bussey Institution

IN an earlier paper* it has been shown that among chinchilla rabbits there occurs a modification of the agouti hair pattern in which the subterminal white band of the agouti hairs is about twice as wide as in the normal agouti pattern, and that this character is inherited as a Mendelian recessive alternative to normal or narrow-banded agouti. It has been shown also that this modification is not due to a change in the agouti gene itself, i. e., to a new agouti allelomorph, but to the action of a modifying gene borne in the same chromosome as the agouti gene. It will be shown further that the linkage between these two genes, agouti and wide band, permits about 30 per cent of crossing over between them.

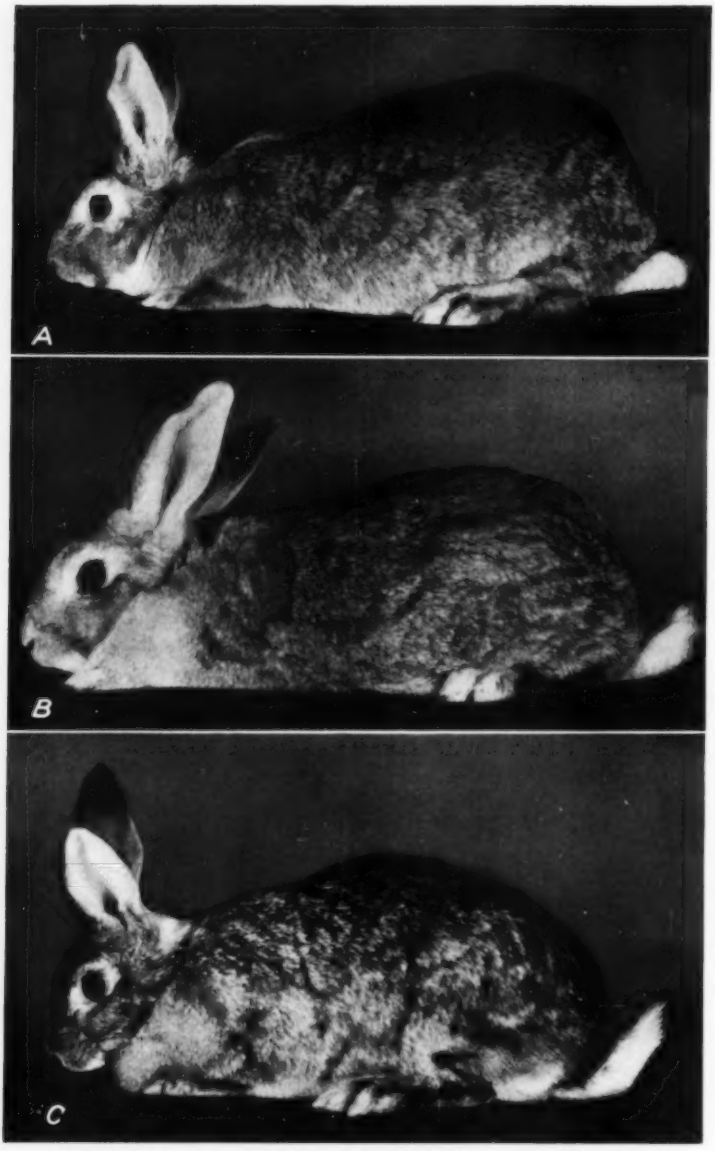
The first indication of such association came from a small F_2 population produced by narrow-banded F_1 parents derived from a cross between a wide-banded agouti individual (*Aw*) and a non-agouti individual of narrow-banded ancestry (*aW*). The F_1 animals were thus of the genetic constitution *Aw . aW*. They produced 6 narrow-banded to 5 wide-banded agouti offspring (besides 9 non-agouti young). Under free segregation of *A* and *W*, narrow-banded should be to wide-banded young as 3:1; under close linkage, as 1:1. It is evident that the latter relationship is the one more nearly approximated in the observed result, 6 narrow-banded to 5 wide-banded.

In view of the possible occurrence of linkage thus suggested, backcross matings were made to test the matter more fully. An F_1 male (*Aw . aW*) was mated with non-agouti females heterozygous for wide banding. There resulted 21 narrow-banded agoutis : 19 wide-banded agoutis : 28 non-agoutis. The expectation here is that with free segregation narrow-banded will be to wide-banded as 3:1, but with complete linkage the two classes should be equal. In reality equality is more nearly realized than the 3:1 ratio, supporting the hypothesis of linkage.

Matings were next made between heterozygous narrow-banded F_1 females (*Aw . aW*) and non-agouti males homozygous for wide band (see Table I, item 1). There resulted 26 narrow-banded : 50 wide-banded young, equality being expected if free segregation occurs, but only wide-banded young being expected if complete linkage occurs.

A different type of F_1 female (*AW . aw*), produced by crossing a narrow-banded agouti female with a non-agouti male homozygous for wide banding, was backcrossed with the non-agouti father (see Table I, item 2). There resulted 54 narrow-banded to 19 wide-banded young, the expectation being equal numbers of each sort if free segregation occurs, but only narrow-banded young being expected if linkage is complete. In reality wide-banded young did occur, but fewer than free segregation would demand. Thus incomplete linkage is again indicated.

*SAWIN, PAUL B., 1932. Albino allelomorphs of the rabbit with special reference to blue-eyed chinchilla and its variations. Carnegie Inst. Wash. Pub. No. 427. Part II.



NORMAL AND WIDE-BAND CHINCHILLA RABBITS

Figure 5

A—A normal narrowbanded chinchilla. *B*—A widebanded chinchilla. Compare with *A* as regards intensity of pigmentation especially in the head region. The wide band gives such individuals a pronounced lighter appearance. *C*—A widebanded chinchilla having darkening modifiers which affect the tip of the guard hairs and render the animal as dark in appearance or darker than a normal narrowbanded individual. The under fur of this specimen shows a typical wide band.

Another group of F_1 females of different ancestry but likewise of constitution *AW* . *aw* was mated to double recessive males (*aw*), producing 46 narrow-banded to 19 wide-banded young (see Table I, item 3). This experiment also shows the occurrence of linkage, since crossovers (19) are notably fewer than non-crossovers (46).

A combination of all backcross matings between a doubly heterozygous individual and a doubly recessive mate is made in Table I. It shows that in each of the backcross matings crossovers were significantly fewer than non-crossovers. There is thus cumulative evidence of linkage between the gene for agouti and the recessive modifying gene which produces wide banding. The sum total of crossovers recorded is 64, that of non-crossovers is 150, which gives an indicated crossover percentage of 29.9 ± 2.3. The deviation from equality (which would be expected, if no linkage existed) is 43, which is 8.7 times the probable error, 4.9, and is thus demonstrative of the existence of linkage. It should be noted that the estimate of the crossover percentage is based solely on the progeny of doubly heterozygous females. It may be expected that doubly heterozygous males will give a slightly lower percentage of crossovers as is known to be the case in other mammals (rats and mice).

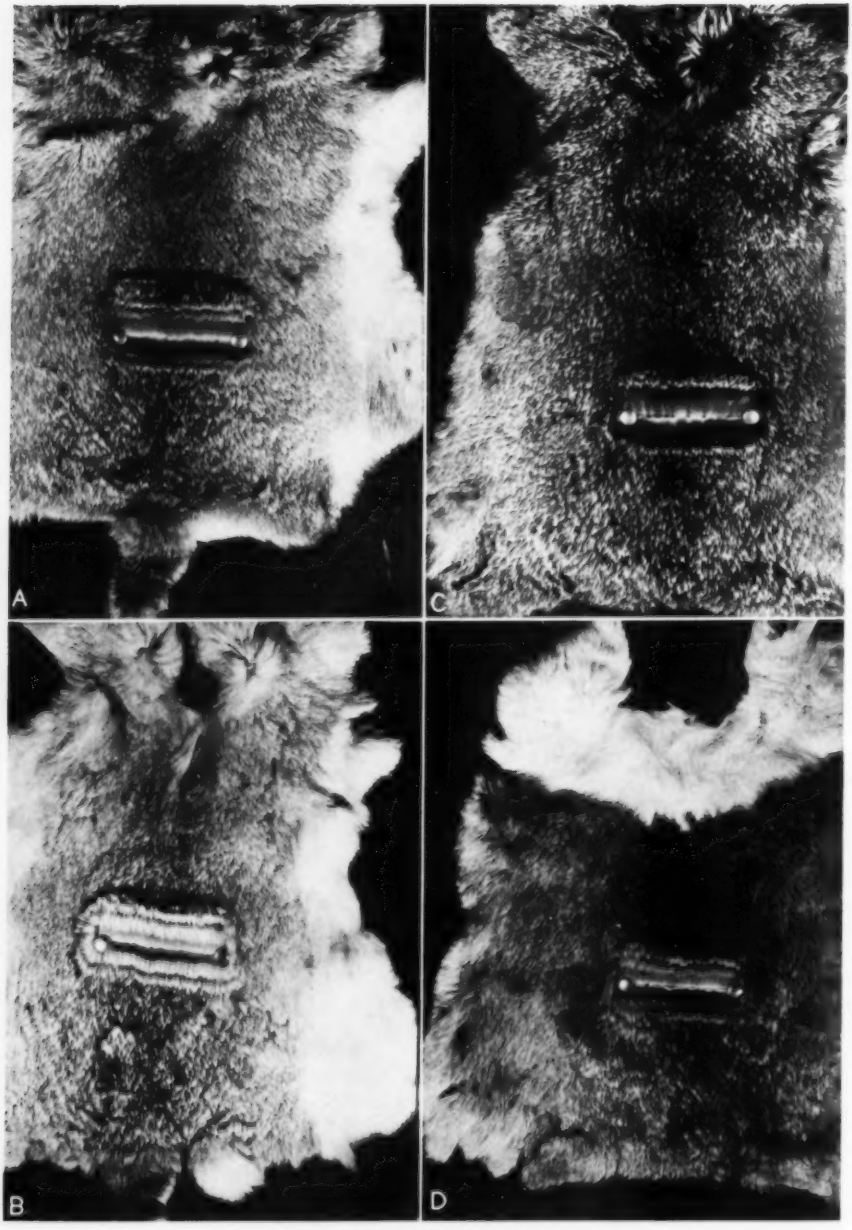
"Wide Band" and "Steel"

Wide band has been described as an agouti modifier whose effect is to increase the width of the yellow or white subterminal band of the secondary guard and wool hairs. In normal agouti rabbits bearing either the full color gene (*C*) or one of the three chinchilla allelomorphs which have been used in these experiments, this band is approximately 5 mm. wide; whereas in the wide-banded individuals the width of the band is just about doubled (see Figure 6, *A* and *B*). This gene is not the first to be described which affects the width of the agouti band, since the well known allelomorph "steel" (E^D) of the extension series is a similar modifying gene, whose presence in the simplex condition greatly reduces the agouti band, and in the duplex condition may entirely eliminate it (compare *A* and *C*, Figure 6).

The interaction of these two pairs of genes has been determined by crossing wide-banded agouti animals (*AEww*) with black rabbits of the constitution AE^DE^DWW. As expected, the F_1 consisted of ordinary steel grays. In F_2 six phenotypes are to be expected as follows:

1.	*A*	E^DE^D	*W*	Black
2.	*A*	E^DE^D	*ww*	Black?
3.	*A*	E^DE	*W*	Normal steel
4.	*A*	E^DE	*ww*	Wide-banded steel
5.	*A*	*EE*	*W*	Narrow-banded agouti (normal)
6.	*A*	*EE*	*ww*	Wide-banded agouti

In several litters thus far produced at least five well defined classes have been found. Besides the well known blacks, normal steels with gray bellies(Figure 6*C*), and the two classes of agouti (narrow-band, Figure 6*A*, and wide band, Figure 6*B*, both of which have white bellies), there is a class obviously steel, having the typical gray belly but with the agouti band approximately 5 mm. wide, typical of the normal narrow-banded agouti (*AE*). See Figure 6*D*. Several does of this type have been mated to a wide-banded (*AEww*) male, and the progeny have consisted of two classes, 50 per cent like the mother and 50 per cent like the father, demonstrating that the mothers are genetically of the genotype AE^DEww. It has not been possible up to this time to identify the combination AE^DE^Dww. In at least the heterozygous condition both E^D and *W* are accessory modifying genes which reduce the width of the subterminal agouti band in agouti rabbits, whereas *E* and *w*, as



EFFECT OF THE WIDE-BAND GENE

Figure 6

Four pelts with fur parted to show the width of the agouti band. *A*—Normal narrow band (*AEW*). *B*—Wide band (*AEww*). *C*—Normal narrow-banded steel (*AE^{D}W*). *D*—Wide-banded steel (AE^{D}Eww). The wide-banded gene produces a band of white near the tip of the hair about twice as wide as that typical of this band in the normal agouti coat.

the respective allelomorphs, increase its width.

It should be pointed out that a certain amount of variation exists in the width of the agouti band apart from the influence exerted by these two genes. In the steel and in narrow-banded agouti combinations such variation is less apparent, but in the wide-band combinations their effects appear to be magnified. It is thought that this gene (w) will furnish an excellent background upon which some of these variations may be studied. By selection it has been possible to produce narrow-banded agoutis so dark as to resemble steel agoutis superficially although they are *AAEE* genotypes, as indicated by the white belly characteristic of agouti rabbits and as demonstrated by their breeding behavior. Correspondingly dark individuals have also been obtained in wide-banded combinations (Figure 5*C*). In this case the typical wide band is found in the under-fur, but the black tip of the hair is increased in length and, because of its superficial position, renders the animal as dark as or darker than the ordinary normal narrow-banded agouti in outward appearance. In the linkage studies described above, darkening modifiers, introduced by the non-agouti parent, have rendered many animals difficult to classify until the juvenile coat has been completely shed.

Selection in the opposite direction, in wide-banded combinations, has resulted in animals in which the pigment has been so greatly reduced as to remain only on the tip of the hairs and on a narrow basal margin next to the skin. Such animals appear very nearly white. A further study of this variation is in progress.

Summary

Wide band, previously shown to be inherited as a simple Mendelian recessive to normal or narrow band has here been shown to be linked with agouti, with a crossover value of approximately 30 per cent. Wide band is hypostatic to non-agouti and supplements the action of E and E^D by increasing the width of the subterminal white (or yellow) band of the secondary guard and wool hairs of agouti and steel-agouti rabbits. Wide band appears to offer a desirable background for further studies of the factors influencing the intensity of pigmentation of the agouti or wild type color pattern in the rabbit.

TABLE 1. Results of backcross matings between doubly heterozygous females and double recessive males to test for linkage between the genes for agouti and wide banding.

F_1 parent	aW young	aw young	aa young	Crossovers	Non-crossovers	Percent crossovers
1 $\frac{+w}{a}$ x $\frac{aw}{a}$ (repulsion)	46	50	70	46	50	34.8±3.0
2 $\frac{+W}{a}$ x $\frac{aw}{a}$ (coupling)	64	19	77	19	64	22.9±3.0
3 $\frac{+W}{a}$ x $\frac{aw}{a}$ (coupling)	46	19	41	19	46	29.0±4.0
Totals				84	160	29.0±2.0

Hereditary Defects of Fingernails and Joints

TWO most interesting family histories of hereditary defect of the fingernails and of the joints are recorded by Dr. John W. Turner, in the *Journal of the American Medical Association* for March 25, 1933. In both these families the nail defects are inherited for four generations as typical dominant characters. In one family all the individuals who had a nail defect also had extensive and characteristic defects of the joints. The kneecaps were so rudimentary as to be almost absent. So abnormal in development were the elbows as to make it impossible to straighten the arm. Many other

joints were affected. In the second family nine members were observed in whom the nail defect was present but in whom the joints were normal in development.

Dr. Turner points out that in earlier family pedigrees which have been recorded of defects in the nails other ectodermal derivatives have frequently been affected. Thus, icthyosis (scaliness of the skin), overdevelopment of hair or its absence, and premature or late eruption of the teeth have been noted as coexisting manifestations of inherited nail defects. Mental deficiency has even been included in the list of congruent defects. Since the nervous system originates from ectodermal tissue of the embryo all these affections can be grouped as variations of a single layer of embryonic tissue. The skeletal system, derived from the embryonic mesoderm, is not affected in these other families. In the two families reported by Dr. Turner, however, there are no other ectodermal abnormalities except the extreme reduction or absence of the nails. All other defects are of the bones and of the joints. The segregation of skeletal and fingernail defects in one family is a further point of considerable interest to human genetics. The evidence from the first family would lead one to believe that the manifestation of all these defects is due to a single gene. The distribution of the two defects in the second family might be taken to indicate that the most likely probability seems to be that the first family is homozygous for a second gene which in the second family only part of the members carry. This is, on the basis of the slight information available, purely hypothesis, but it conforms to the facts fairly well.

This secondary gene which controls the skeletal defect might be considered a "modifier of dominance" gene somewhat similar to the frizzle modifier in fowls reported recently by Landauer. In the presence of the modifier the defective gene may become nearly recessive, affecting only the nails.

More recently Turner's suggestion of the existence of two independent inherited genes has been criticized by Aschner (*Journal of the American Medical Association*, June 6, 1934). She presents data from twelve other families, observed by herself and from the literature, in which various combinations of the characters in question appear. In some of these the patella and all the fingernails are defective; in others, only the thumb nail is affected; in others the patella, the nails, and the head of the radius all are affected. In another family camptodactyly ("crooked little fingers") is also included in the syndrome.

Aschner believes that the facts can best be explained by assuming that all these various elements are conditioned by different genes located on the same chromosome. In some families the defective allelomorph of only one of these genes is present. In others, two or more of these defects are inherited as a linked syndrome, with crossing over between normal-bearing and defect-bearing chromosomes accounting for occasional instances of a break-up of the usually associated characters.

At least one serious objection can be raised against such a view. As yet, observed genetic linkages in man other than sex linkage, have been few and far between—in fact those that have been claimed have later appeared more questionable. Possibly such a syndrome represents a grouping of genes ideally adapted to demonstrate linkage. On the other hand, the fact that many careful studies have failed to reveal any close linkage in man, must make us skeptical that all at once we are likely to come on a group of possibly five rather closely linked genes. The facts at hand would seem as satisfactorily explained by one or more modifying factors. Such an explanation is possibly less improbable than so much linkage all at once, though Aschner's suggestion may be the correct one in spite of probabilities.

R. C.

THE TOOTHLESS MAN OF SIND

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IN a previous issue of this JOURNAL the writer[7] reported the occurrence of a toothless type of man, the "Bhuda" of Hyderabad (Sind). The abnormality is hereditary and is apparently due to a recessive sex-linked gene, since the daughters of affected fathers transmit the defect to half their sons. Since then more cases of hereditary tooth defects have been reported by Ovazza,[4] Beade,[1] Huskins,[3] Roberts,[5] Schultz,[6] and Clark and Clark.[2]

A few more facts about the "Bhudas" of Sind have been collected and are reported herewith. A photograph is presented, giving a close view of the mouth opened wide to show the absence of teeth.

The peculiar defects of the "Bhudas" are:

(1) They do not have teeth either deciduous or permanent. In some cases a few of the molars made their appearance. While the teeth are absent, the jaws of these persons are fairly strong from childhood so that they are generally able to masticate and digest their food.

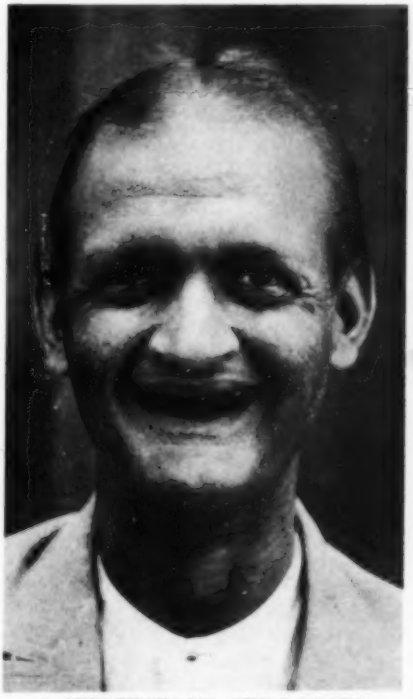
(2) The hair on their heads is usually light in color, soft, silky, and short, growing not more than six inches in length. There is a characteristic bald spot on top of the head.

(3) They are very sensitive to heat and do not perspire on account of the absence of sweat glands in the skin.

(4) These persons possess similar round faces, flat noses, and thick lips.

Their origin and history so far as it is known may be briefly described as follows:

The "Bhudas" of Sind are known to be descended from one ancestor and the youngest members of this group may be said to belong to the sixth generation. No records either written or from memory are available about the first two generations. According to the family records the third generation consisted of an affected brother and



A HEREDITARY SEX-LINKED TOOTHLESSNESS

Figure 7

Example of the type of toothlessness and deficient hair development conditioned by a sex-linked recessive gene found in certain parts of India. The character has spread from a single toothless male through his female descendants, so that in the fifth generation it has appeared in the male progeny of twenty of the original "Bhuda's" great granddaughters.

normal sister, apparently a "carrier." Their maternal grandfather was probably a "Bhuda," the character first appeared in him as a recessive mutation. These two persons of the third generation seem to have spread the character in the Amil Community of Hyderabad (Sind). There were eight families having affected members of the fourth generation and this number increased to twenty in the fifth generation. Even more affected individuals have appeared in the sixth generation.

Inheritance

The affected man of the third generation had a normal wife and produced in the fourth generation seven sons and five daughters who were to all appearance normal. The sons of the affected man married normal girls and produced in the fifth generation all normal children whether males or females. The daughters of the affected man married normal men and in fact, no case is known where a girl carrying the defect has married a "Bhuda" since intermarriage between blood relations is prohibited in this community. Half the sons in the fifth generation were abnormal but all the daughters were apparently normal except one who was partially abnormal. The behavior of the fifth generation children, as judged from the progeny of the sixth generation, was the same as that of the preceding generation. However, the partially abnormal girl of the fifth generation produced from a normal husband one abnormal daughter in the sixth generation. Unfortunately this was her only child, as she died shortly after its birth.

The sister of the affected man of the third generation was married to a normal husband and produced in the fourth generation three children: two sons, both abnormal, and one apparently normal daughter. The "Bhudas" of the fourth generation behaved in the same manner as their maternal uncle of the third generation in producing all normal children in the fifth generation. The apparently normal girl of the fourth generation transmitted the abnormality to half her sons in the fifth generation. In this line of descent also, there appeared two abnormal girls in the sixth generation, one from a fifth generation affected male and another a fifth generation female who was apparently normal.

The occurrence of these exceptions in the inheritance of an abnormality due to a sex-linked recessive gene has been previously reported by Huskins who has described a dental abnormality consisting of the absence of the two center incisors of both upper and lower jaws from both sets of teeth. The manner of inheritance of this defect was the same, and in that case too a variable dominance of the defect was reported. Two daughters of an affected man showed the defect while two other daughters transmitted the missing teeth to sons though themselves normal.

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Error in September Number

McKinney and Sando, Recumbence in Wheat: Vol. 25: No. 9; page 356, column 2, line 16; 30-40 degrees should read: *50-60 degrees.*

OFFSHOOTS ON THE FLORIDA SILVER PALM

Reproductive Habit of Florida Species Unique Among North American Palms—of Possible Evolutionary Interest

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THE palms indigenous to the United States do not normally produce offshoots. Recently, however, it has been found that the Florida silver palm (*Coccothrinax garberi*) is unique in this respect for it produces true offshoots.* These occur not only on young trunkless palms but also on the trunks of adult trees. The appearance of this characteristic in a single species possibly represents an example of a mutational change in reproductive physiology.

Although the native cabbage palmetto of Florida sometimes produces branches, and the creeping saw palmetto has branches that might be termed offshoots these branches differ morphologically from the offshoots of the silver palm.

Upon first observation the offshoots of the small, trunkless, silver palms might be mistaken for seedlings and even when pulled up, casual inspection might lead to the conclusion that they were seedlings broken off above the attachment of the roots. Careful excavation and removal of the leaf sheaths of the parent palm discloses that the young plants are attached to the base of the older palm, Figure 9.

During the early stages the offshoots are very similar to young inflorescences but differences become more pronounced as the leaves emerge and roots are formed. The small plants do not remain attached to the older plant after they have formed a root system; the attachment being so delicate that the growing roots exert sufficient force to separate them, Fig. 8*D*, *E*. In this manner thick clumps of young palms are formed around the base of the parent palms, producing an effect that is quite unusual.

On the palms of the mainland offshoots are found only at the base of young trees, but on Big Pine Key offshoots occur not only at the base of young trees but on the trunks of adult trees as well. This geographic differentiation is believed to be wholly environmental, but until palms from both localities have been grown together the possibility of there being geographic races of this palm cannot be eliminated.

The offshoots produced on the trunks of adult palms differ greatly in general appearance, Fig. 8*B*, *C*. Some are similar to inflorescences in having long basal sheaths and in their attachment to the trunk. Others are purely vegetative in form having short basal sheaths and well developed roots but they do not become detached from the trunk as do the offshoots of young palms. The offshoots of the young palms are analogous to those of the Old World date palm (*Phoenix dactylifera*) which latter regularly produces offshoots and indeed is propagated vegetatively by separating them from the parent trees.

Schaffner's theory of sex reversals in the early stages of inflorescence production with an unusual development during the neutral stage may explain the production of offshoots on older palms, but does not apply to the young palms where they occur before the flowering stage is reached.

In the original flower type of the angiosperms, the floral axis passes from a neutral

*This palm was described by Sargent in 1899 without record being made of its production of offshoots. SARGENT, C. S. *Botanical Gazette*, Vol. XXVII, Jan.-June, 1899, p. 90.

OFFSHOOTS OF THE SILVER PALM

Figure 8

A—Large silver palm (*Coccothrinax garberi*) with offshoots, note normal leaves, short, thick trunks and root development of the offshoots. *B-C*—Variation in offshoots on different trees: *B*, offshoots with simple leaves, long basal sheaths, and no roots. *C*—Offshoots with short enlarged bases, normal leaves and roots well developed. *D-E*—Detailed views of offshoots. *D*—A small silver palm with an offshoot almost disconnected by the force of the growing root. *E*—An offshoot producing other offshoots.

ORIGIN OF OFFSHOOTS

Figure 9

A young silver palm with offshoots arising from the short horizontal root-stock. The offshoots are nourished and protected by the parent palm and can live under conditions that would prove fatal to a seedling. This specialization adds greatly to the chances of the palm's survival in fire swept regions, as in southern Florida. Offshoot at the left of the trunk showing the attachment to the trunk by a broad base. Natural size.

state to the secondary male state and then by a prompt reversal to the secondary female state. In various primitive types of such flowers, however, the reversal of the growing flower bud from the male to the female condition is rather slow so that a considerable neutral development takes place in the transition which may manifest itself in several ways.*

Collins has observed and recorded variations in maize that may be analogous to offshoots on palms.

While these young plants, being produced in the place of regular sexual organs, may properly be called apogamous, yet this phenomenon is closely related to the common forms of asexual reproduction, particularly to that observed in some of the small varieties of maize that produce ears at the surface of the ground. Several such cases have been observed in which roots were developed on the lower nodes of these ear-bearing branches and the ear was able to continue an independent existence after the main plant was dead, the husk leaves acting as assimilating organs.†

The possibility that offshoots are formed during the neutral stage of sex reversal seems plausible, or perhaps they represent a normal function of a vigorously growing silver palm, just as in the date palm of the Old World. The writer, however, is inclined to believe that asexual reproduction or a modified form of apogamy is the most logical explanation because the offshoots that form on the trunk of the palms, considered from the standpoint of asexual reproduction, are analogous to the maize variation except that in the case of the palm, the inflorescence which includes both male and female floral organs, is replaced by only one plant whereas in maize, the male inflorescence which is separate from the female inflorescence produces numerous small plants, one for each spikelet.

Another indication of asexual reproduction, especially in the palms with trunks, is that during the period of offshoot production the palms appear to be sterile, that is, the inflorescences are replaced entirely by offshoots. No normal inflorescences were found on either the small or the adult palms in the space occupied by offshoots, though some of the palms had passed through this stage and had resumed the production of normal inflorescences. From the general external appearance of the offshoots, the basal attachment to the trunk, the long basal sheaths, the flattened appearance, and their occurrence on the palms in the axils of the leaves, it might be supposed that they were inflorescences in which the floral primordia had developed into leaves.

The rooted offshoots from the small palms, if separated carefully to avoid breaking the roots, should transplant readily. On the large palms, after the basal portion of the offshoot enlarges and roots are formed, it is believed that an independent existence is possible, Figure 8*C*. Further study and experiments with the offshoots may show that the palms can be readily propagated in this way which will be a great advantage over seed propagation since the silver palm grows extremely slowly and the old palms rarely survive transplantation from their native habitat.

*Schaffner, John H. 1933. The Production of Vestigial and Sterile Sex-Organs Through Sex-Reversal and Neutral Sexual States. *Bulletin of the Torrey Botanical Club*, 60:89-97.

†Collins, G. N. Apogamy in the Maize Plant. *Cont. to the U. S. Nat. Herb.*, Vol. XII, Part 10, July 21, 1909.

INHERITED SUSCEPTIBILITY TO ACUTE MASTITIS IN CATTLE

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THE Alaska Agricultural Experiment Stations, with headquarters at Sitka, began in 1917 the crossbreeding of Holstein and Galloway cattle with the purpose of producing a hardy dairy cow. The work has progressed to a point where calves of the fourth and fifth generation are being born. During the course of the experiment three cases of acute mastitis occurred amongst related animals. This suggested the possibility that susceptibility to the disease is inherited.

The three animals concerned were a dam, daughter and granddaughter, and in all three the mastitis was so severe that the udders eventually became entirely non-functional. A purebred Galloway cow, No. 140, Bertha A, Reg. 34889, mated to the Holstein bull, Chimacum Sir Quirinus Cornucopia, Reg. No. 1746468, produced an F_1 female No. 21, her only daughter. This F_1 female, No. 21, was later mated to the F_1 bull, No. 33 (her half-brother on the sire's side) producing the F_2 female, No. 48, also an only daughter. All three of these females, dam, daughter, and granddaughter, exhibited similar clinical symptoms of the disease.

Both the dam and the daughter had udders that, from the standpoint of dairy quality and conformation, would be judged rather undesirable. The dam's udder was pendulous and meaty in texture, while No. 21, the daughter, would be criticized for having not only a loosely hung, pendulous udder, but one of poor conformation, and deficient in size. The granddaughter, No. 48, on the other hand, had an udder the appearance of which was rather desirable from a dairy standpoint, and could be criticized chiefly for being too loosely hung posteriorly to the body.

The dam, No. 140, lost the left rear quarter of her udder early in her second lactation, due to what was at the time believed to be a chronic case of mastitis. The right rear and right front quarters were affected and gave no milk in her third lactation, and the remaining left front quarter became non-functional during her fourth lactation. The daughter, No. 21, lost one quarter in her first lactation, a second quarter in her second lactation, and the remaining two quarters so early in the third lactation that she was fattened and slaughtered after having been milked less than thirty days. The granddaughter, No. 48, gave 5109.3 pounds of milk in the 287 days of her first lactation, which began when she was 33 months old. She seemed perfectly normal when finishing her first lactation, the only possible exception being that the lactation period was somewhat short of the usual 365-day period reached by a number of the F_1 and F_2 heifers. However, beginning with the sixty-third day of her second lactation, an aggravated case of mastitis developed and the entire udder was lost. Both of the calves dropped by No. 48 were males. Except for these three cases no example of mastitis of such marked virulence was found in any of the several hundred other cows bred by the Alaska stations. The original purebred Galloway cow, No. 140, had been bought, and nothing was known

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†Contribution No. 106 from the Department of Animal Husbandry.

concerning the occurrence of mastitis among her ancestors.

According to Hucker*, it has been estimated that about eight cows per thousand per year have the acute, or clinical, type of mastitis. He makes the following significant statement:

> One interesting observation in connection with the clinical type of mastitis is the fact that it rarely spreads through the herd. It occurs in isolated instances, and, although the cow has been in the milking line previous to infection, adjoining cows rarely become infected.

The sub-clinical (sub-acute, chronic, latent, etc.) form of mastitis, however, is much more prevalent, and in certain tested New York herds Hucker states that from 20 to 90 per cent of the individuals have been found to be infected. In this form, also, he is of the opinion that the evidence indicates that its spread by contagion or infection is comparatively rare.

Both the observations of Hucker and the results herein presented agree with the assumption that predisposition to acute mastitis is inherited, and, based on the three cases cited, it also seems legitimate to assume that one or more dominant genes are responsible for the susceptibility. There is the possibility that susceptibility to the milder forms of mastitis is inherited, but no evidence on that point is available at present. Until more critical data are obtained it seems useless to theorize on the possible inter-relationships of the genes affecting susceptibility to the two main types of mastitis.

It has not been mentioned previously that both the daughter, No. 21, and the granddaughter, No. 48, had full brothers, and that none of them was retained for breeding purposes since they were not of the type desired in the original experiment. If one had been kept, there would have been a fairly good possibility that he was at least heterozygous for the postulated dominant gene (or genes), and in that case one would expect a large proportion of the daughters to have mastitis of the acute type. Bulls from such mothers are rarely retained for breeding in any herd.

The results herein presented are not by any means conclusive. The main purpose is to call attention to the problem, with the hope that data of a more critical nature will be accumulated eventually by other workers. If the results are amply verified, and the mode of inheritance of the susceptibility therefore definitely known, it will mean that the geneticist can be of more value than the veterinarian in producing dairy animals free from this objectionable disease.

The Technique of Obtaining Family Histories

An outline for the study of Physical Diagnosis and History† which calls attention to the importance of gaining the sympathy and understanding of the patient in order to secure an accurate family history. Since such data are often the source for the study of human inheritance, this technique could well receive emphasis in medical training.

HELEN COOK

*HUCKER, G. J. 1933. The laboratory detection of bovine mastitis. New York State Agricultural Experiment Station, Geneva, *Bulletin* No. 626.

†CLENDENING, LOGAN. *The Laboratory Notebook Method in Teaching Physical Diagnosis and Clinical History Recording.* C. V. Mosby Co., St. Louis, 1934.

THE NORDIC IN AMERICA

BETWEEN the field of exact quantitative studies in physical anthropology or human heredity and the general public there is a no-man's land of discussion either oral or written into which the author possessed of a venturesome spirit, a thick hide and a sense of humor occasionally dares to venture. Sometimes he is activated by boredom, or idle curiosity; sometimes by the need of capitalizing sensationalism; sometimes by the profound belief that he has a vital message to deliver. The author of *The Conquest of a Continent** has for decades been classified, by friend and foe alike, as belonging to the last named group. For this reason his most recent book may fairly be recognized as a presentation of his point of view on a debated and controversial question—namely, the essential value of the traits, which by common usage have come to be described as Nordic, in the building of our national life.

He appears admittedly as an advocate for the qualities which the Nordic is defined as possessing. He attempts to prove his point and to convert or convince his reader both by positive evidence for Nordic worth and by direct or indirect evidence that other types have done less of permanent value. As Henry Fairfield Osborn points out in the introduction, the book's objective is to prove that "in its origin and evolution our country is fundamentally Nordic."

The reviewer has made no attempt to audit the accuracy of the statistics on which much of the book depends. He is sure that the author has made every reasonable effort to obtain and use only accurate data. Those whom the author has associated with him in preparing and editing the book have an excellent reputation in this regard. The reviewer therefore has proceeded in the belief that statements of fact contained in the book are correct, and will limit himself to a discussion of the important general implications of the book, which deal with the question of the racial and cultural future of America.

It is an outstanding quality of the book, as a whole, that the history of the development of the country is given in considerable detail. Migrations and the acquisition of territory—involving as it frequently does, new racial and social elements — are carefully chronicled in detail.

The interpretation of the value of these various developments is the first point at which the opinion of the author becomes an important factor. This opinion is always given frankly and in unadorned phrases. It is therefore bound, in the very nature of things, to prove irritating to a number of our citizens.

The purely polite, rather than biological, value of the Spanish influence on our Mexican immigrants, the arrival of "large numbers of ignorant and destitute South Irish Catholics" and the demoralization of "our municipal governments" by the descendants of this same group are not likely to pass unchallenged.

Yet in spite of his evident partisan position the author has provided any thinking citizen with ample food for contemplation. It cannot be denied that this country, especially in the face of hard times and a changing social order, must choose what standards it cares to follow.

The implication underlying the author's development of his subject is that much of our "freedom" of speech and press has been and is fictious. This, in turn, can only mean that our much vaunted and frequently emphasized "tolerance" is in truth merely a very comfortable and lazy ignoring of the various intolerances which certain racial and religious groups have introduced. In times of plenty for all and with a scattered population, the existence within

*GRANT, MADISON. *The Conquest of a Continent.* Price $3.00. Charles Scribner's Sons, New York, 1933.

our boundaries of groups of alien ideals and creeds is not an important issue. The possessor of vast acres of cultivated and productive crops can better afford to neglect small plots of weeds than the man whose existence depends upon the productive utilization of every available inch of soil. The author obviously senses the future danger of continuing our old *laissez-faire* policies. In this attitude experience bears witness to his sagacity. The long fight for more restrictive and selective immigration laws is now a matter of history. Those who had first-hand knowledge of this development need no further illustrations to recognize the elements of vital truth in the author's thesis.

To any one whose descendants must experience the problems of the future the book is really a necessity. If, as the past has repeatedly shown, human nature in crises shows little change in the passage of centuries, conflict of some sort is certain to ensue. Whether mere numbers will decide the issue or whether a relatively small intellectual aristocracy will rule the future state is a matter of pure conjecture. Human Biology, dictating the recognition and utilization of human quality — Economic Greed, blowing its bellows on the red hot metal of class consciousness—Religious Fanaticsism, sneaking and skulking behind vast and powerful organizations—are giants observing our civilization as it writhes and twists in the meshes of unsound thinking and overorganization. Of the three, Human Biology—though it may be new and untried and though its decisions will be scientific rather than emotional—seems to be the truest friend to man. Both of the others have ruled him in the past and have always betrayed him.

It may be fairly objected by some that Mr. Grant is not a biologist and that therefore his classification of "race" and interpretation of the lasting qualities that he terms "Nordic" are not—in an experimental sense — scientific. Even though this be granted, however, there is such a quality as common sense which can as fairly be used in discussing racial problems as can the statistical methods which have become a fetish to so many. No one can have any reasonable doubt concerning the point which the author is really trying to make. For the purposes of the argument it makes no very great difference whether the qualities that he considers Nordic are inherited or are transmitted by direct contact from generation to generation.

The reviewer, therefore, welcomes Mr. Grant's book as a bitter and undisguised stimulant to the jaded tongue of a tired and bewildered people. It may blister or irritate; it may even be spit forth in disgust by some; but it will leave none of its readers as inert and indifferent as they were when they picked it up.

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SEX FROM AMOEBA TO MAN

DR. CURT THESING is a biologist with a wide acquaintance with the relevant literature and with a decided flair for presenting facts and opinions in an attractive manner. In this, his latest book,* he surveys the field of sexuality from amœba to man. The book is well written, always remembering that it is addressed to the general public and meant to persuade its reader to adopt a certain attitude towards matters of sex; the translation is excellently done and the illustrations, photographs and line-drawings are truly astonishing.

There are many who will agree heartily with Dr. Jelliffe, who in his introduction states his view that "most men and women would be far better equipped to comprehend and solve such perplexing problems as arise in their own

*Thesing, Curt, *Genealogy of Sex*, $5.00. Emerson Books, Inc., New York, 1934.

lives and in the lives of those around them, if they had a greater understanding of the origin and development of the sexual impulse," and who with him will welcome this book as one which, being read, must lead to such understanding. On the other hand, there will be others who perhaps will conclude that the book does not provide the most suitable approach to an understanding of the nature of human sexual behaviour for people with educational systems and social backgrounds different from those of the Germans in whose language this book was originally written. The biologist will certainly find in it a most attractive presentation of the different copulatory mechanisms and behaviours to be found in the animal kingdom. But will the troubled adolescent, unaided, find that serenity which follows the removal of a sense of sin, from a study of the vigorous photographs of copulating lions, storks, emues, toads?

The earlier chapters present an excellent and popular account of the facts of sexuality, starting with the unicellular organism which as a whole takes part in the reproductive act and ending with the separation of certain cells within the individual for the special reproductive function, passing rapidly through the intermediate hermaphrodite stage. The biologist will find much to provoke his disagreement; the sex-chromosome sex-determining mechanism, the time law of intersexuality and its application to the case of the hermaphrodite, for example, receive scant and imperfect treatment, but after all this is not a scientific text-book and every one will agree that to make these matters simple is indeed difficult.

Next follows an enchanting chapter on the amatory life of hermaphrodites and one is drawn to Meisenheimer who studied every detail of the love play of the edible snail. In the chapter on the awakening of the sexual impulse there is given a most graphic description of the migration of the salmon and the eel and the reader now knows that the author can write and the translators translate. The book is as exciting as a good novel. In "the emancipation of woman" the story of the spider, the mantis and the bee, misinterpreted, may lead to much domestic strife for few men will read of the fate of the male in intercourse without developing strong views on the relation of the sexes in human society. The married man with a grouse will find useful ammunition here. "Lures and Stimuli" is an excellent elementary account of the mechanisms of attraction but it is incomplete for since it was written much more knowledge relating particularly to the ape and the rat has become available. For this analysis of the phenomena in human beings the author makes use of the case of the Trobriand Islanders, and though the account is in a way interesting it is doubtful that there is much in it that can be applied to the problems of an industrialised urbanised society.

A pleasantly written popular book, this: no one could read it without encountering something of which he had been previously ignorent. Did you know that at the Sorbonne, a sum of ten million gold francs is held in trust, this having been a prize offered more than a century ago by an eccentric to the first man who became pregnant? I didn't.

F. A. E. Crew

University of Edinburgh

Prescription for the Millennium

I believe that the wholesale regeneration which so many seem to expect cannot be affected appreciably by tinkering with the institution of property, but only by taking in hand life, and trying to build a new race. That would be the starting point for an ideal for the law. The notion that with socialized property we should have women free and a piano for everybody seems to me an empty humbug.—Justice O. W. Holmes.

BLOOD GROUP DISTRIBUTION OF THE AMERICAN INDIANS

"Islands" of Atypical Tribes Suggest Repeated Mutations

MUCH work has been done on the racial distribution of the three allelomorphic genes whose interactions result in the four main blood types: *O*, *A*, *B*, and *AB*. These observations have been put forth as having a considerable, though as yet undetermined, diagnostic value as evidences of racial relationship. A discussion of the evidence this technique gives regarding the origin and migration of the American Indians concludes a recent report on the blood group distribution of three hundred individuals from ten tribes of Indians living along the coast of British Columbia.* Of this group 260 were *O's*, 38 *A's*, and two *B's*. In several of the tribes it was known that those showing the *A* blood type were related and one five generation pedigree is given showing typical dominant inheritance. Gates also gives summaries of other reports on Indian blood groups from North and South America. These give a significant picture of preponderant *A's*, a smattering of *B's*, and a trace of *AB's*, (except in a small sample from Tierra del Fuego which shows three *O's* and thirty *B's*). This is in agreement with previous reports on the blood group distribution of the American Indian summarized by Snyder† as 91.3% *O*, 7.7% *A*, 1% *B* and 0% *AB*.

It has been held that the high percentage of the *O* blood-group among American Indians is an indication that the progenitors of the Indians had separated from a parent racial stock somewhere in Asia before the *A* mutation and the *B* mutation had occurred,—both *A* and *B* being dominant to *O*. Conclusions based on such reasoning are rendered distinctly hazardous by reason of the deplorable and widely noted tendency for a given gene to repeat the same mutation from time to time. Direct comparison of percentage distribution of the blood group genes may for this reason be of little value, and an "island" of one type in a preponderating region of another type might be taken to be due to race crossing or to a new mutation.

Two possible examples of such independent mutations have recently appeared in the literature. Matson and Schrader (*Journal of Immunology*, August, 1933) report that in two tribes of Plains Indians the distribution of the four groups notably departs from the usual picture of preponderant *O's*. Among 115 in one tribe, pure Blackfeet, only two blood groups were found: 23.5% *O* and 76.5% *A*. Among 24 pure Blood Indians the percentages were approximately the same, 16.7% *O* and 83.3% *A*. In neither group were any *B's* or *AB's* found. In both these tribes a certain number of Indian-white hybrids were also tested, and distributions intermediate between these and that characteristic of the white race were observed.

Still another situation is found in the Caraja Indians of Brazil. Golden (*Lancet*, 1930) found in 61 members of this tribe the following distribution: 39.0% *O*, 5.0% *A*, 51.0% *B*, and 5.0% *AB*. This is in close correspondence with the Fuegian series reported by Gates and additional data from this region might define the boundaries of a rather large "island" showing a preponderance of *B's*. In this sample a higher percentage of *B* is encountered than in the European races, and consequently the presence of the *B* gene could hardly be accounted for on the

*Gates, R. R., Blood Group and Physiognomy of British Columbia Coastal Indians. *Journal of the Royal Anthropological Institute*, 64: 23-44, 1934.

†Snyder, L. H., *Blood Grouping in Relation to Clinical and Legal Medicine*. Williams and Wilkins, Baltimore, 1929.

basis of crossing with Europeans, were it alleged in explanation that the Indians tested were not of pure blood.

As an example of parallel mutations in man the two woolly-haired Nordic mutations reported in the JOURNAL in recent months may be cited. It would appear that the unusual blood group distributions discussed above might reasonably be accounted for by such an occurrence. Other blood group "islands" owing their origin to such independent mutuations may well be discovered as more information becomes available. If this happens with the blood groups it is an excellent explanation of the situation noted above. The chances of survival of such mutations would seem to depend primarily on the size of the group in which they occur because none of the blood groups seems to confer any selective advantage in increased vigor or immunity to disease.

That such mutations may occur is also suggested by the fact that in any large series of parent-offspring blood group tests a certain small proportion of cases is found which do not conform to the rules of mendelian heredity. These are accounted for as being due either to illegitimacy or to errors in technique. Doubtless most of these cases can be correctly ascribed to one or the other of these sources of error, but it is also conceivable that a certain small proportion of these inconformities might be due to mutation. This possibility would render such incomformable cases of especial interest. Those due to faulty technique could, of course, be eliminated by retesting the subjects. The elimination of cases due to illegitimacy would obviously be much more difficult. The application of a polysymptomatic test applying as many independently inherited mendelian characteristics as possible, ought to indicate in a good many cases, that the alleged parents could not be the actual parents of the child, and these cases could then definitely be ascribed to other causes than mutation. This would leave a small number of cases which might still be due to illegitimacy but which also might be due to mutation, and the intensive study of these cases would be both a challenge to the experimental ingenuity of the investigator and his diplomatic finesse in arriving at conclusions of scientific value without landing either in a hospital or in a court of law. If any venturesome soul attempts to explore this obviously complicated territory he may have much reason to be thankful that an understanding of the laws of mendelian inheritance (and of their possible implications) is still as lamentably restricted as is actually the case.

Gates suggests that the gradually increasing complexity of the blood group relations may add to their value in racial diagnosis. Thus the recent discovery in Scandanavia of two distinct A types (A_1 and A_2) may make it possible to differentiate the A's in various parts of the globe. Gates notes also that the Australian aboriginees have an agglutinogen which is not found among Europeans. Nothing is known about its distribution in other parts of the world, but it may well prove useful in differentiating certain racial groups. The recently discovered M and N agglutinogens have already been found to be distributed unevenly in the various divisions of the human race. Thus by taking account of the distribution of all these different types and subtypes a very illuminating classification of the various races of mankind may be possible. Much still remains to be learned about the distribution of the four primary blood groups and practically nothing is known about the distribution of the newly discovered M-N differences in blood reaction. If the races of man were in a state of static equilibrium, there might be more hope of learning enough about these immunological peculiarities to make them useful in deciding which races are which, but with modern transportation the hope of obtaining information regarding even the rather doubtfully pure races that now exist becomes less each year.

R. C.

A BUD SPORT IN FLOWER FORM

Figure 10

A fig tree in Riverside, California, which has three branches bearing short-styled caprifigs, and one branch (left) bearing long-styled edible figs. Such anomalies may help us to understand the evolutionary steps that have given rise to the edible fig.

ANOMALOUS FIG TREES

Plants Showing Chimaeral Differences in Flower Form of Value in Throwing Light on the Origin of Edible Figs

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IN my recent paper* on "The Structure and Development of Flowers in *Ficus carica*," I pointed out that the facts regarding the nature of the fig and of the caprifig and the habits of the pollinating insect are of common knowledge to growers of Smyrna figs and to practical horticulturists of fig districts but are somewhat shrouded in mystery or lacking in clarity to many others. This is not at all surprising since published accounts of the fig tree are often confusing and occasional anomalous forms of the fig only serve further to confuse the matter.

A single fig tree normally bears receptacles or syconia each lined on the inside with pistillate flowers, all of which are either distinctly long-styled or all distinctly short-styled. This is one of the fig fundamentals which readily serves to distinguish the edible fig (with long-styled flowers) from the caprifig (with short-styled flowers). In the syconia of *Ficus carica*, well-developed staminate flowers are associated with short-styled pistillate flowers only. Leclerc du Sablon† reports, however, finding flowers with rudimentary stamens in the same receptacle with long-styled flowers. He also reports finding a continuous series of flowers ranging in length from those with short styles to those with very long styles. Previous investigators have found rudimentary pistils in occasional staminate flowers but my paper in 1932 shows that such rudimentary pistils are normal and not exceptional. Such studies of anomalous flowers help to reveal the phylogenetic development of the common fig from primitive forms into the various classes now recognized.

In a block of some three thousand seedling fig trees at the University of California Citrus Experiment Station, Riverside, there are two trees different, I believe, from any so far recorded. One tree, a cross between Kassaba and the Excelsior caprifig, has four main framework branches, one bearing receptacles with short-styled flowers, and three bearing receptacles with long-styled flowers. The second tree, a cross between Kadota and a caprifig of *Ficus palmata*, has three branches bearing short-styled caprifigs and one branch bearing long-styled edible figs. There is no indication in the main trunks that two seedlings have become naturally grafted together during the transplanting process, that is, each tree is from a single seed. In both cases the single branch bearing receptacles different from those on the other three branches, may be considered as a bud sport.

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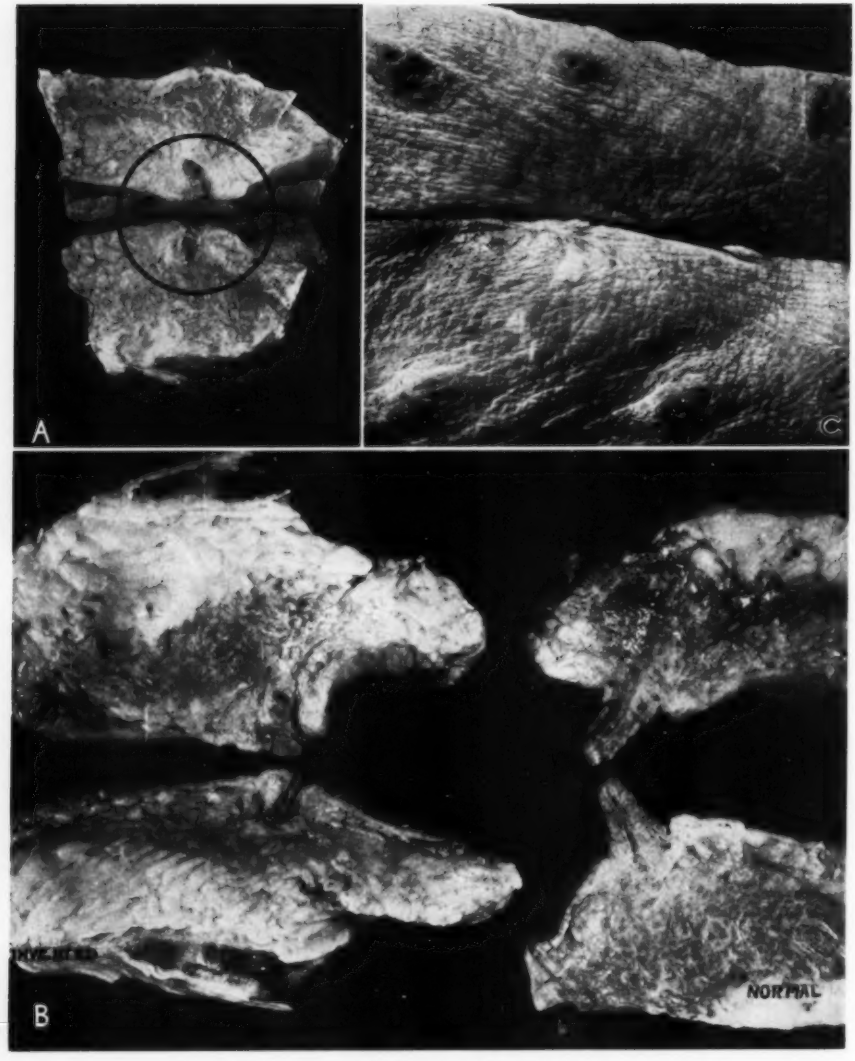
*CONDIT, I. J. 1932. The Structure and development of flowers in *Ficus carica* L.—*Hilgardia* 6(14): 443-481, figs. 1-10.

†LECLERC DU SABLON, M. 1908. Observations sur les diverses formes du figuier. *Rev. Gen. Bot.* 20: 129-150; 207-216. 15 figs.



INVERTED AND NORMAL NIPPLES

Figure 11

A—Cross section of an inverted nipple. *B*—Cross section of inverted and normal nipples. *C*—Five inverted nipples found on a single individual. The inverted nipples derive their name from the fact that they extend inward instead of outward as the normal nipple does. The normally external part of the nipple is telescoped and its tip is within the breast. This is clearly shown in the illustration above (*B*), where the tip of the inverted nipple is indicated by an arrow. Note that the inward-extending pit of the inverted nipple is about equal in depth to the extension of the normal nipple.

CONGENITAL DEFECTS IN THE MAMMAE OF SWINE

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THERE are a large number of variations in the nipples of swine and other mammals. Some of these are of considerable importance because they affect the functional ability of the nipple. In the polymastic mammal, as for instance the sow, there are marked variations in the arrangement of nipples.[6] Any significant variation from the uniform spacing of nipples is undesirable. Variations occur in the form of unequal numbers in the two rows. It is not unusual to find too much space in front of the first pair of nipples and a crowding of nipples toward the rear. In a number of cases observed by the author the first pair of nipples is located in the normal position of the second pair. In practice two objections are usually listed against this, first, that the pigs while suckling are crowded too much toward the rear where there is more danger of becoming injured, and second, that the nipples toward the rear are the least productive. In all probability the arrangement of nipples is influenced by heritable factors. Figure 12*A* shows the spacing of nipples in a normal sow.

There are likewise many variations in nipple shape, some of which do not particularly influence functional efficiency. On the other hand there are some shapes that seriously affect the ability of the nipple to function normally. Some nipples are "cone shaped" and others are "stunted." In the latter case the nipple extends only a little beyond the surface of the breast and is often too short to be of practical use. The "mushroom," "mulberry" and "fissured" types are of ample size as a rule. The terms used to identify them are descriptive of the shapes involved.

The "hollow" and "inverted" types are often spoken of as "crater" nipples because they are telescoped, forming a cavity in the surface of the breast (Figure 11*C*). There is a difference in the degree of inversion in these two types. In the hollow and inverted types the nipples are retracted (Figure 11*A*). Mistakes are often made in identifying these two types. In a number of cases nipples that may appear inverted when the female pig is five or six months old are later extended to normal length. This extension of the nipple takes place usually during the latter part of gestation or the first day or two of lactation. The hollow type may be a variation of the inverted nipple and the possibility of the nipple being extended may depend on the degree of inversion. Typically inverted nipples have not been extended by a number of practical methods of manipulation (see Figures 11*A* and *B*).

Total suppression of nipples in swine is common. This type of defect has been reported in cattle by Turner,[5] and Heizer.[2] In the human, Creighton[1] has reported that "complete absence of both mammae is one of the rarest of congenital deformities." Cases of congenital retraction of nipples in the human are rather common in surgical reports.

Defects may also occur in the form of openings along the side or at the base of the nipple. Williams[7] has observed openings at the base of the mammae in the human. Openings

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along the side of the nipple are not uncommon in cattle.

Economic Importance

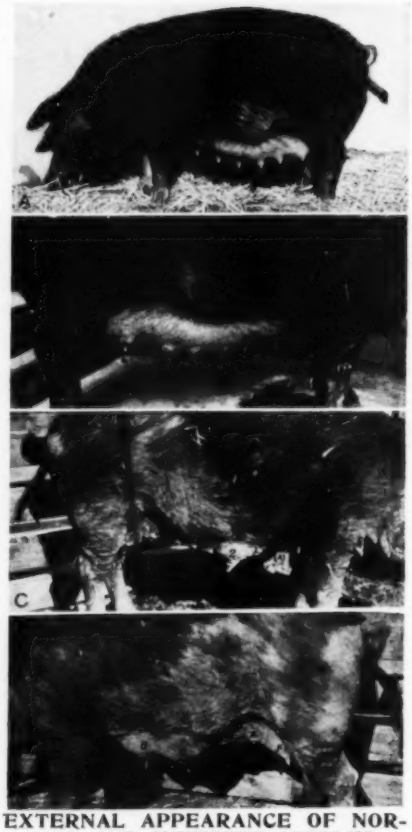
The sow shown in Figure 12*A* has six normal, properly spaced nipples on each side.[3] In contrast to this, Figure 12*B* shows a sow having only two normal nipples on the right side and three on the left. The photograph was made two days before term. Figure 12*C-D* shows the right and left sides, respectively, of the latter sow after she had been suckled for a period of eight weeks. In Figure 12*B* it may be noted that nipples 2 and 6 are normal and 1, 3, 4 and 5 are inverted. In Figure 12*D* nipples *B*, *C* and *F* are functional, *E* rudimentary, and *A* and *D* inverted. This sow had five normal and eight non-functional nipples. She farrowed fourteen pigs and suckled only five, one of which was overlaid at four weeks, allowing nipple 6 (Figure 12*C*) to dry up. Some of her pigs were "farmed" out to another sow. It is impossible for pigs to suckle effectually a typically inverted nipple.

There is a possibility that gland troubles are more likely to occur when the nipples are non-functional. In a survey of mammary gland trouble in the human, Williams observed that "out of 97 cases of acute mammary abscess there was imperfect development of the nipple in 48." However, there has been no gland trouble encountered so far in the sows that have been used in this study.

The inverted nipples are usually found in the middle of the nipple rows. When only one inverted nipple is present very rarely is it found toward the rear of the nipple row. The number of pigs which a sow mothers is usually limited to the number of her normal nipples.

Description of Inverted Nipple

An inverted nipple resembles a pit or crater in the breast. The depth of the pit varies. Figure 12*B* shows



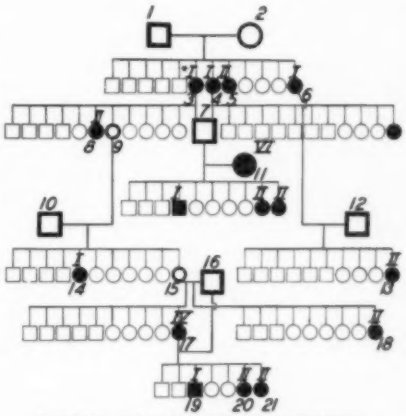
EXTERNAL APPEARANCE OF NORMAL AND INVERTED NIPPLES
Figure 12

A—Normal development of the nipples of a sow, showing uniform spacing. *B-D*—Three views of a sow with defective nipples. *B* shows the right side of this sow two days before the birth of her first litter. *C* and *D* show the right and left sides respectively of this individual after eight weeks of suckling. The nipples on the right side are numbered, and those on the left side are lettered for convenience in distinguishing them. On the right side only two nipples (2 and 6) are normal, the other being inverted. On the left side three nipples are functional (*B*, *C*, and *F*). The others are inverted. The tendency toward the production of these inverted nipples is inherited, probably as a mendelian recessive character.

five inverted nipples on the same individual. By comparing the two halves of a normal nipple sectioned through the

lactiferous ducts (Figure 11*B*), with inverted nipples (Figure 11*A*, *B*, and *C*), it will be observed that the depth of the pit is almost equal to the extension of the normal nipple. The inverted nipples in these two figures have been sectioned through the center of the pit. The lactiferous duct openings of the inverted nipple in Figure 11*B* is indicated by an arrow.

The inverted nipples do not seem to be associated with lack of gland development. It will be noticed in Figure 11*A*, and in Figure 11*B* ("inverted"), that the gland development is quite equal to the gland development in the normal specimens shown in Figure 11*B*. This observation is substantiated, at least superficially, by the uniform enlargement of the glands to be noted in Figure 12*B*. The gland was as fully developed for each of the inverted nipples as it was for the extended nipples. The "filling" at the base of the nipple, which usually precedes term by a few days, was typical for all nipples. The vascular zone of the nipple is apparently contiguous with the gland tissue, and the thin dermis, which normally covers the entire exterior of the nipple, lines the cavity in the inverted nipple.



INHERITANCE OF INVERTED NIPPLES

Figure 13

The Roman numerals indicate the number of inverted nipples on the individual in question. That the defect is inherited seems to be established by the large number of cases observed of this family. The mechanism of inheritance is however not definitely determined.

Cause of Defect

No effort has been made so far in this study to determine the embryological development of the defect. Williams has found in the human at an early stage of development that the site where the nipple will subsequently appear is marked by a depression, toward the bottom of which the ducts of the gland converge. If, however, this rudimentary state persists, malformations result. The same investigator has further observed that the development of the nipple from the rudimentary depression is affected by the area of the skin perforated by the ducts being raised up into the form of papilla above the level of the rest of the integument. Turner[4] has found, in working with the mammary gland of cattle, that "the teat develops as a result of the active proliferation of the mesenchyme cells surrounding each mammary bud gradually raising the bud above the surface of the surrounding epithelium." If this same type of nipple extension or evagination obtains in the mammae of swine it would seem that the cause of the defect can be explained by the presence of an inhibiting influence that arrests the mesenchyme cell proliferation so that the mammary bud fails to rise above the surface of the surrounding epithelium. If further investigation substantiates this point of view, it would seem that the defect is subject to genetic analysis.

Inheritance of Defect

Inverted nipples in swine have been observed by the author for a number of years. The defect was rather noticeable in one linebred strain. This strain is represented in the pedigree chart, Figure 13, by the mating of boar 1 to sow 2. The results indicated are rather characteristic of the

occurrence of the defect in this strain. The strain is sufficiently linebred to permit recessive factors to appear. Sows 3, 5 and 6, in a number of matings to boar 7, repeatedly produced pigs with inverted nipples. When sow 17 was bred to boar 16, her own sire, the number of affected individuals was somewhat larger than the number produced in the litter in which she was farrowed.

It is rather difficult to make a final analysis of inverted nipples in pigs at birth for reasons noted previously in this paper. The inverted nipples in the affected individuals in the chart persisted to maturity. In all probability the ratios in the chart would have been somewhat different had all the pigs been developed to maturity. Some pigs were overlaid and it seemed desirable to reject cases that could not be definitely measured.

From the data available so far there seems to be no doubt that the defect is inherited. Sufficient data are not available to afford an analysis of the probable influence for the location of inverted nipples in the nipple row.

Summary

Data on a new congenital defect in swine in the form of inverted nipples have been presented.

The inverted nipples are of considerable economic importance because they are non-functional and especially because they may occur in large numbers on the same sow.

Typically inverted nipples cannot be extended by practical means of manipulation.

The defect is obviously inherited, and the data seem to indicate recessiveness.

The hereditary influence functions probably as an inhibitor to normal nipples.

In order to eliminate the defect it appears necessary to avoid the use of animals that are affected or that are the parents of affected offspring.

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Soda Straws in Hybridizing Cotton

In the May, 1934, issue of the Journal Doak described a new method of emasculating cotton and of protecting the stigma by slipping over it a short section of a soda straw, which was fastened in place with a paper clip or string. After Dr. Doak's method was published it was found that a small amount of lint cotton wrapped about the base of the stigma is easier to use and is more satisfactory in holding the soda straw fast and in keeping out insects than the paper clip or string. The soda straw should be slipped down over the lint cotton with a slight twisting movement. Beginners usually encounter difficulty because they try to use too much lint.

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A Glossary Of Technical Terms

Used In This Issue

GENETICS has developed so rapidly that many terms in common use in genetic literature are not yet incorporated in the dictionaries. Many people who are interested in heredity are bothered by such words, for which no definition can conveniently be found. For this reason, it is proposed to publish occasionally a glossary of terms which would not be readily understood and which are not to be found except in new unabridged dictionaries (and often not there!). It is realized that these definitions will probably not meet with universal approval and comments and suggestions will be welcomed.

AGGLUTINOGEN—A substance from which an agglutinin is produced; which in turn, is a substance which has the property of clumping and precipitating certain specific types of blood corpuscles or bacteria.

AUTOSOME—Any chromosome except the sex-chromosomes.

CHROMONEMA—A fine thread of chromatin material from which arises the spireme thread.

CROSSING OVER—Interchange of segments between two homologous chromosomes previous to the formation of gametes.

DIPLOID—Having the normal paired chromosome arrangement found in somatic tissue, due to doubling of the primary chromosome complex at fertilization. See *Somatic*.

EPISTATIC—Non-allelomorphically dominant; i. e., "Dominance" refers to the interaction of two or more genes located at the same point on the chromosomes. Epistasy refers to dominance relations of two genes situated on different chromosomes.

HOMOLOGOUS—Chromosomes occur in somatic cells in pairs; the members of these pairs are spoken of as homologous chromosomes.

HYPOSTATIC—Non-allelomorphically recessive. (See *Epistatic*.)

MEIOSIS—The reduction divisions preceding the formation of gametes, in which the chromosome pairs separate, and the chromosome number in the resulting daughter cells is reduced to half the somatic number. As distinguished from ordinary cell division (*mitosis*) in which each chromosome splits longitudinally to furnish a full complement of (paired) chromosomes to each of the daughter cells.

METAPHASE—The middle stage of cell division when the chromosomes are grouped in the equatorial plate.

MUTAL TRANSLOCATION—Reciprocal transfer of parts of two non-homologous chromosomes, as an exchange of fragments from the ends of the second and third chromosomes. (Essentially crossing over between non-homologous chromosomes.)

MUTATION—Where a heritable variation begins. A sudden variation in an inherited character.

ONTOGENY—The developmental history of an organism, from fertilized egg to adult individual.

PHENOTYPE—The organism as exemplified by its expressed characters, as contrasted with its genetic constitution (the genotype).

PLASMOSOME—A true nucleolus of a cell.

PLASTIN—A viscous difficultly soluble nitrogenous substance found in the nucleus of cells.

PROPHASE—The stage in cell division prior to the metaphase, during which the chromosomes appear in the nucleus, following the resting stage.

SEGREGATION—Separation of allelomorphic genes at meiosis.

SEX-LINKED—Applied to characters carried on the sex-chromosomes—characterized by typical peculiarities in inheritance as a result of this fact.

SOMATIC—Referring to body tissues; having two sets of chromosomes, one set normally coming from the female parent and one from the male; as contrasted with germ cells having a single set of chromosomes.

SYNAPSIS—The conjugation or union in pairs of homologous chromosomes, respectively of maternal and paternal origin, to form bivalents; the primary step is reduction or meiosis. (Wilson.)

TRANSLOCATION—Attachment of a fragment of one chromosome to a non-homologous chromosome, resulting in a new arrangement of genes.

TRIPLOID—An organism characterized by having three times the reduced primary chromosome number.

ZYGOTE—A fertilized gamete. Produced by the fusion of sperm and ovum. A new individual in the single-cell stage.

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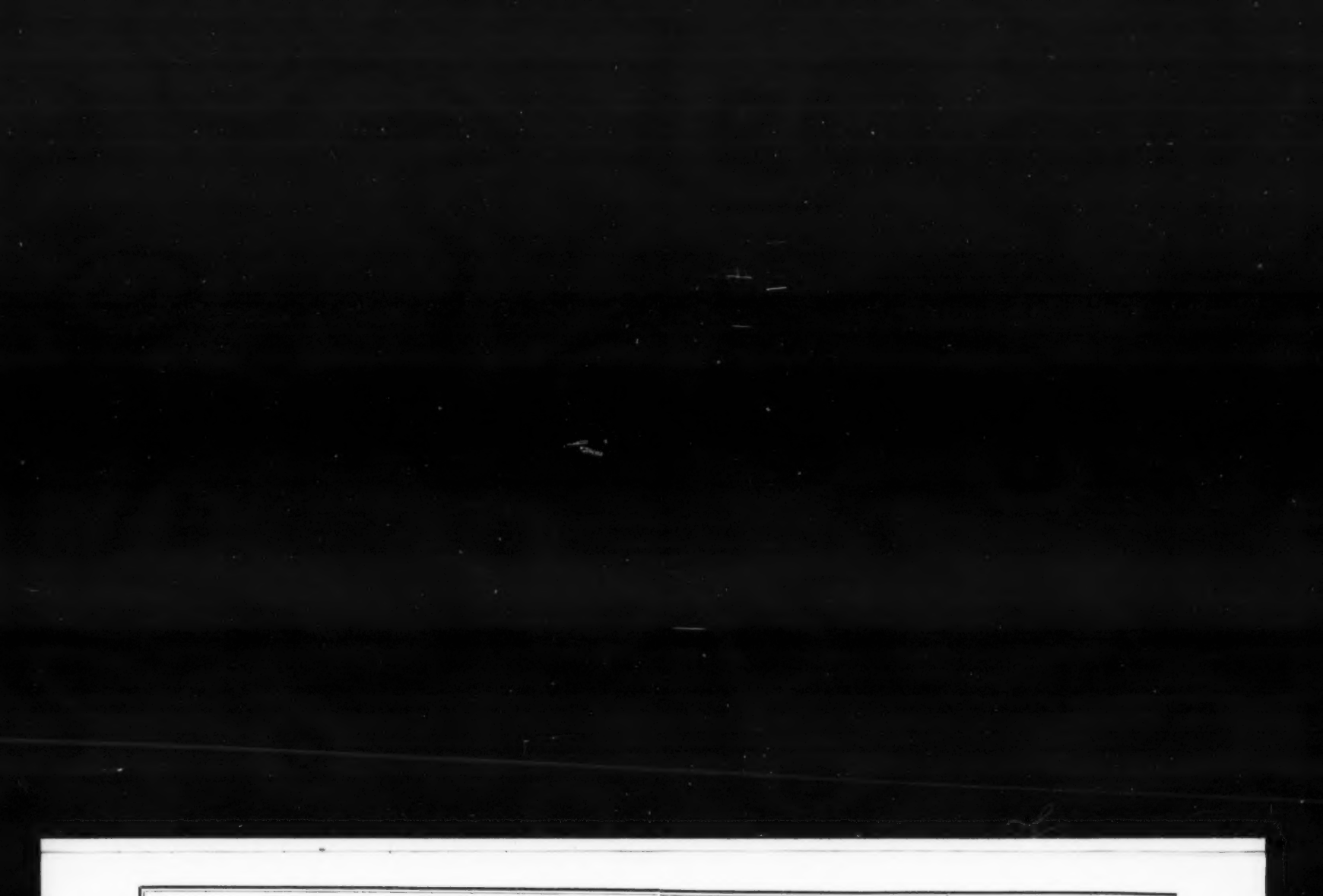
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